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The role of proximate factors in shaping individual cognitive variation of great tits

Thesis presented by

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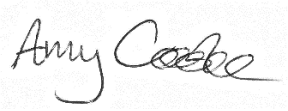
Declaration

This is to certify that the work I am submitting is my own and has not been submitted for another degree, either at University College Cork or elsewhere. All external references and sources are clearly acknowledged and identified within the contents. I have read and understood the regulations of University College Cork concerning plagiarism.



Amy Cooke

Abstract

Cognition is defined as the mechanisms that allow animals process, store and act on information. These mechanisms mediate behaviour and how animals interact with their environment. Yet not all individuals behave the same. While much of this variation may be attributed to differences in cognitive abilities among individuals, our understanding of why individuals vary in cognitive performance is limited. Examining the factors that drive individual variation in cognition is fundamental for understanding its adaptive significance, particularly when factors that determine how well an individual performs on a task may or may not be heritable. The aim of my thesis was to investigate how a range of distinct and understudied proximate factors shape individual variation in cognitive performance in great tits (*Parus major*) across different problem-solving and cognitive tasks. Using a multi-access problem-solving device to test sequential innovative problem-solving performance, I discovered that food-related motivation drives innovativeness and likelihood of solving, while previous experience drives accuracy and that individuals show repeatable differences in their accuracy and ability to solve. Between individual differences in problem solving performance were explained entirely by accuracy, motivation, and positive feedback loop caused by previous experience. Food is fundamental for survival and reproduction and food quality impacts cognition and behaviour. In my third chapter I found that diet correlated with problem-solving success, while personality correlated with the proportion of arachidonic acid, an ω-6 polyunsaturated fatty acid that is crucial for normal development and functioning of the brain. Great tits experience varying levels of predation risk as they forage in complex and fluctuating environments, but little is known about the effect of predation risk on learning and cognition in the context of foraging. In Chapter 4 I show that under high predation, birds demonstrated greater behavioural flexibility compared to those under low predation risk and displayed worse spatial memory for their reward location than those under medium or low predation risk. In Chapter 5 I take the spatio-temporal learning paradigm into the wild, and explore the effects of species, age and distance between feeders on discrimination and temporal learning. I show for the first time in the wild that both great tits and blue tits are capable of temporal and reversal temporal learning, but performance in any of these metrics were not correlated among individuals. Shorter distances between feeders resulted in faster discrimination learning

performance, but had no effect on temporal learning. My thesis demonstrates how a variety of underexplored proximate factors explain individual variation in cognitive performance, emphasising the challenges faced when measuring cognition generally but especially in the wild.

Acknowledgements

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Chapter 1. General Introduction

For many animals, cognition mediates the interaction between behaviour and the environment (Shettleworth, 2009), and in the face of increased global environmental destruction and modification, examining the forces that drive individual variation in cognition is fundamental for understanding the adaptive significance of cognition (Wong and Candolin, 2015). Since its emergence in the 1980s, behavioural ecology has enabled researchers to identify and examine the adaptive significance, and thus evolutionary importance, of animal behaviour (Cate and Healy, 2017). To understand the adaptive significance of cognition, i.e. whether cognitive traits are units of selection, whether they can be selected for and whether there are trade-offs between cognitive ability and other traits, they must be studied across many different contexts. If we are to answer the pertinent question as to why some animals are more intelligent than others, we must be able to define cognition. Shettleworth (2009) defines cognition as the mechanisms whereby animals process, store and act on information from the environment. This broad definition touches on the concept that intelligence encompasses several different kinds of cognitive mechanisms. These include, for example, spatial learning, behavioural flexibility and inhibitory control. Years of research in the field of comparative cognition have aimed to identify and define these various cognitive mechanisms using model laboratory animals (Pearce, 2013). However when wild animals act on information from the environment to, for example, find food, avoid predators or interact with social group members, there may be several cognitive and non-cognitive traits driving their behaviour (Griffin and Guez, 2014; van Horik and Madden, 2016; van Horik et al., 2017). As a result, a challenge in cognitive ecology is to identify what traits underly behaviour, and because animals cannot talk to us, we must infer their mental processes through observed behaviour (ten Cate, 2014). To overcome this challenge, we must measure cognitive performance in carefully constructed, validated tasks that tap into specific cognitive mechanisms of interest. And so, the aim of this thesis is to investigate how a range of distinct and understudied proximate factors shape consistent differences between individuals in cognitive performance.

Cognition and ecology

The study of animal cognition stems from comparative psychology, and in the first half of the twentieth century, it centred around testing the learning capacity of specific species (Dewsbury, 2000). This classic research was primarily focused on two general lines of study. First, Thorndike (1898) used problem-solving experiments to demonstrate that cats were capable of trial and error learning, by placing them in puzzle boxes, and timing how long it took for them to press the correct lever to escape. Over successive trials the duration to solve became increasingly shorter, demonstrating that cats were capable of trial and error learning. The second line of study was associative learning, involving tasks such as conditional learning, whereby animals learned to associate a behaviour with a neutral stimulus (Pavlov and Thompson, 1910), and operant learning, where behaviour was reinforced either through reward or punishment (Skinner, 1938). The aim of these studies was to test and discover the extent of the learning capacity of a given species. Following these early studies, research turned to "higher" cognitive mechanisms that were considered uniquely human abilities, with a view to understanding how cognition evolved across species, such as episodic memory, causal reasoning, and theory of mind. This type of in-depth investigation was indispensable for discovering individual cognitive capacity, however basic cognitive mechanisms were given little consideration in these studies and it was assumed that behaviour was driven by associative learning. Furthermore, these early studies were constrained by small sample sizes (Dewsbury, 2000) and the tendency to focus on high performing individuals (Wasserman, 1997). Consequently, the results were not representative of the species as a whole, nor could findings be extrapolated to other species. In order to address these constraints, experiments began to shift focus to the underlying cognitive mechanisms driving behaviour, how these mechanisms vary between species (Washburn, 1926; Wasserman, 1993), and their relevance in ecological processes.

Cognitive ecology brings together cognitive science and animal behaviour (Real, 1993) in order to understand interspecific cognitive variation, and encompasses a vast range of observed behaviours, from spatial learning (Brodin, 2010) and tool use (Auersperg et al., 2011), to communication (Wenner et al., 1967) and cultural transmission (Aplin et al., 2015). The aim of cognitive ecology is to test how cognitive mechanisms are distributed between species (a mechanistic framework) and how

socioecological factors may drive cognition (a functional framework) (Healy and Braithwaite, 2000). The functional framework centres around the concept that the cognitive abilities of a given species have been conserved because of the natural history of that species. For example, coal tits (*Parus ater*) outperform great tits (*Parus major*) across a number of spatial learning and memory tasks (Krebs et al., 1990) because of the ecological and natural history of these species, where coal tits cache food items and can store and relocate cached food throughout the day, or across a number of days, whereas great tits are non-storing and consume food as and when they find it. The mechanistic framework involves detailed study of the intricate cognitive processes required to generate that behavioural outcome, and may entail on cognitive mechanisms between species or cognitive variation within species. For example, Clayton and Dickinson (1998) discovered scrub jays (*Aphelocoma coerulescens*) have episodic-like memory, defined as memory of a past personal experience which involves three separate recall mechanisms, what (discrimination learning), where (spatial memory) and when (temporal learning). Through a carefully designed experiment they demonstrated that scrub jays used these three forms of memory (what, where and when), to retrieve previously stored food. However, studies investigating intraspecific cognitive capacities may be limited by a failure to distinguish between cognitive ability and performance (Reichert et al., 2020), and a high dropout rate which may result in emphasising high performing individuals (Thornton and Samson, 2012). To combat this, increased sample sizes are needed for a better representation of population-level variation within species. Recent technological advances such as automated feeders with individual identity tracking mean that we can measure behavioural variation in insects (Schneider et al., 2012), fish (Ferrari et al., 2014), birds (Bridge et al., 2019) and mammals (Rose et al., 2020) at even finer scales, with minimal human disturbance, and in doing so we can measure how individual, ecological and contextual factors shape cognitive performance.

What are we measuring: ability or performance

Distinguishing between ability and performance is central to understanding cognitive mechanisms underlying behaviour. Cognitive performance - the realised outcome of a cognitive test at a given time, may differ from cognitive ability - the full potential of an individual's cognition. This distinction is important when inferring the causes and consequences of individual differences, particularly if performance is sensitive to task-

specific details, such as environmental factors (Quinn et al., 2016), motivation (Birch, 1945), physiological states (Boogert et al., 2013), and previous experience (Ebel and Call, 2018). One approach to examine whether a cognitive test is an accurate measure of individual's ability is to test for temporal and/or contextual consistent individual differences in cognitive performance, known as repeatability (Cauchoix et al., 2018). A second approach is to manipulate both cognitive (e.g. experience) and non-cognitive factors (e.g. motivation) across individuals and directly test how they affect performance on tasks aiming to test a specific cognitive mechanism (Logan, 2016a). A third approach for understanding individual differences in cognitive performance is to test for links between cognitive performance and non-manipulated traits such as physiology and performance on distinct cognitive tasks to infer relationships that may be driving cognitive performance (Farine et al., 2015). By using these approaches, I aim to address the extent to which proximate factors and environmental variables contribute to cognitive variation and its consistency across repeated measures.

Traditionally, data analysis centred on the "adaptive mean" as representative of a cognitive ability for a population or species (Dall et al., 2004; Rowe and Healy, 2014). Thus unexplained variation around this mean was dismissed as 'noise', and more variation was considered as detracting from the robustness of the group measure (Carter et al., 2013a; Weiss and Adams, 2013). Consequently, this approach ignored the fact that variation was present at the individual level – variation that should be viewed as the unit on which selection is acting within a population. Additionally, cognitive performance was rarely measured in the same individual more than once because multiple measures from the same individual were not accounted for statistically and therefore no longer independent. Research has now shifted focused to individuals differences (Thornton and Samson, 2012), by using new statistical methodology such as mixed models and repeatability analysis, in combination with multiple sampling of performance measures (Boogert et al., 2018; Cauchoix et al., 2018). Therefore it is possible to interpret what proportion of this previously unexplained variation (i.e. noise) in the data is accounted for by consistent differences between individuals' cognitive performance.

Repeatability

Repeatable between-individual differences in cognitive traits provide the empirical framework for studying the long-term implications of behaviour such as heritability and evolution (Dingemanse et al., 2002), and are associated with foraging rates (Chittka et al., 2009), mating success (Keagy et al., 2009) and reproductive output (Cole et al., 2012; Cauchard et al., 2013). Sokal and Rohlf (2013) define repeatability as the proportion of the total variance accounted for by differences among groups and is calculated as

$$Vbetween/Vbetween+Vwithin$$

where V is the variance. The sum of variance between and within individuals accounts for the total phenotypic variance. However, there are some challenges related to the measuring of repeatability in the context of cognition. The first challenge associated with collecting multiple measures of cognitive performance is standardization of measures, because previous experience may influence cognitive performance (Chapter 2). For example, when measuring repeatability in innovation, the first observation of a novel behaviour is a measure of innovation, whereas the second instance of the exact same behaviour from that individual is no longer novel. Despite the observed behaviour being identical in both instances, questions arise as to whether these two measures are comparable, as there may be differing mechanisms driving the outcome, namely experience and/or innovation. The second challenge is that our estimates of repeatability may be confounded by other variables, such that our estimates are falsely inflated. Imagine measuring individuals repeatedly for a resource-dependent trait, such as carotenoid colouration in great tits (*Parus major*). A patchy environment is created because individuals stay within their own territory, but berry density may vary across different territories, creating a patchy environment. As a result, an environmental variable, habitat patch (where individuals stay within their patches), rather than an inherent trait (e.g. genetics) will contribute to the repeatability estimate of great tits' yellow colouration. Furthermore, if offspring occupy the same or similar habitat to their parents, they are likely to have similar carotenoid colouration. However this yellow colouration is resource dependent and thus reversible. This reversibility has implications for cognitive performance versus ability. If performance is solely driven by environmental noise, then how well an individual performs on a task is

meaningless if there is no consistency in how individuals are affected by such noise. However, if there is maintained rank order differences in their performance, despite environmental noise, then this should be shown in repeatability, and therefore, even if confounding variables are present, it is possible to meaningfully interpret their performance and how it relates to the experimental treatment. Thus, before making conclusion regarding the repeatability of a cognitive trait, it is imperative to determine whether a behaviour is mediated by cognition or another trait entirely, and to carefully consider how interactions with environmental factors may influence cognitive performance.

Causes of individual variation in cognition

An animal's cognitive performance may not solely depend upon its cognitive ability. Cognitive performance is affected by multiple factors and is frequently context dependent and highly plastic (Dukas, 2004; Thornton and Samson, 2012; Quinn et al., 2016; Reichert et al., 2020). Ultimate factors are a result of evolutionary forces acting on them (Greenberg, 1998), i.e. through natural selection, these generally do not fluctuate within the lifecycle of an individual (Immelmann, 1972). In comparison proximate factors encompass any factor that varies within the lifecycle of an individual, to instigate or maintain behaviour, and therefore may be key determinants of cognitive performance. They can be broadly divided into two categories; intrinsic or extrinsic factors. Examples of intrinsic factors include traits that vary between individuals such as personality, physiology, sex and age, and/or within individuals such as motivational state, experience, physiology and age. By contrast, extrinsic factors are primarily environmental, such as predation risk, food availability and habitat. Notably, such extrinsic factors may interact with intrinsic ones, such as the effect of food availability on hunger and thus motivation. A fundamental goal of behavioural ecology is to determine the extent to which proximate, ecologically relevant factors shape observable behaviour (Rowe and Healy, 2014). Below I provide details of the different intrinsic factors examined in this thesis, including personality, motivation, and previous experience.

Personality

Personality is defined as a behavioural trait that remains consistent within an individual across different contexts and/or time (Réale et al., 2007), and common

personality measures include exploration in a novel environment and latency to approach a novel object. Personality may determine exposure or rate at which individuals perceive and utilise information in their environment (Smit and van Oers, 2019). For example, in the exploration test, the rate at which an individual moves around a room may generate opportunities to gather more information, in a shorter time frame than individuals that are slow to explore an environment. Similarly, by approaching novel objects in a shorter time frame, they may discover new food or shelter resources. On the other hand, individuals that are slow to explore or approach a novel object may be able to gather deeper knowledge regarding their environment or novel object, which generates a different kind of information gathered or processed (i.e. quality versus quantity). Nevertheless, the occurrence of information processing during personality tests is an underlying assumption, because personality tests neither account for, nor measure, cognitive performance. A meta-analysis by Dougherty and Guillette (2018) found evidence for a small but significant correlation between personality and cognitive performance however the direction of the correlation is highly variable. This would imply that we should continue to account for personality as a factor in cognitive performance.

Motivation

Variation in motivation can occur through either intrinsic or extrinsic influences. Intrinsic motivation is the average baseline motivation of an animal and involves exploration and investigation of an object or environment without any goal or reward (Hughes, 1997), where typically an individual is likely to be relaxed (Ebel and Call, 2018). Knowledge acquired by the animal through intrinsically driven motivation is more likely to be applied across different contests (Call, 2013). In contrast, extrinsic motivation generally has a goal and can be induced in the individual. Behavioural experiments commonly use food deprivation as a form of extrinsic motivation in order to increase participation in the experiment (Griffin and Guez, 2014). Experiments involving this method are often constrained to captive experiments, in order to closely monitor and standardise the food consumption across all individuals. Motivation is often viewed as a confounding variable, if considered at all, when examining mechanisms underlying, for example, problem-solving tasks (reviewed in Griffin & Guez, 2014). Controlling for motivation is complex because even if extrinsic influences on motivation are standardised (Auersperg et al., 2012), individuals may

intrinsically vary in their response to extrinsic motivation. As a result, whether food deprivation removes, or just changes individual differences in motivation and its influence on cognitive performance remains unclear.

Previous experience

Cognitive performance may be a function of previous experience (Rowe and Healy, 2014; Sih and Del Giudice, 2012), through knowledge of past action-outcome contingencies that may influence the current outcome (Birch, 1945; Call et al., 2017). Behaviour may become more efficient through refinement or improvement in accuracy (von Bayern et al., 2009). For example, the completion time in a given task may shorten over successive trials. On the other hand, previous experience may constrain future behaviour, through the "functional fixedness effect" (Ebel et al., 2019), whereby awareness of a prior function hinders current behaviour. For example, once an individual discovers a solution on a multi-access access task, they are less likely to discover a new, potentially more effective solution (Gruber et al., 2011).

Extrinsic proximate factors stem from the external environment, as a result they are, for the most part, less likely to vary between individuals, and therefore can affect multiple individuals at once (Ferrari, 2014). However it should be noted that the extent to which extrinsic factors affect cognitive performance may vary because individuals may react differently to a common stimulus. For example if a startled bird makes an alarm call within a flock of foraging birds, the stimulus (i.e. extrinsic factor) is the same for all other individuals, however there may be variation in how each individual perceives and reacts to it. Below I discuss the specific extrinsic factors examined in this thesis, namely food and nutrition, predation threat, space and time.

Food and nutrition

As stated above, food plays a large role in the motivation to participate in cognitive tasks, and the strength of this factor varies both within and between individuals. Once consumed, food may also continue to affect cognition through nutritional effects, such as increased efficiency of synaptic transmission and modulation of neurotransmitters release (Barón-Mendoza and González-Arenas, 2020), and through its effect on the microbiome, which regulates bidirectional gut–brain communication pathways (Cryan and Dinan, 2012). Of particular relevance are the fatty acids contained in food, that are used to meet to the energetic and physiological demands of the animal (Greenwood

and Winocur, 2005), and some fatty acids like arachidonic acid are vital for the development and functioning of the brain (Wainwright, 2002). Furthermore, from human psychological literature, we know that fatty acid deficiencies are associated with a vast range of psychiatric disorders including depression (Bazinet and Layé, 2014), bipolar (Lotrich et al., 2013) and attention deficit disorder (Janssen and Kiliaan, 2014). Despite this evidence, studies in behavioural ecology rarely focus on the effect of nutrition, however understanding the dynamics between diet and behaviour and underlying cognition could help interpret the causes of individual variation in behaviour.

Predation threat

Predation is arguably one of the main drivers of evolution (Yoshida et al., 2003), affecting population dynamics (Hik, 1995; Turchin, 2003) and driving changes in animal behaviour (Lima and Dill, 1990; Cresswell et al., 2003). An appropriate response to a predation threat is vital for survival. Individuals can be alerted to the presence of a predator through two means, through personal information (Lima, 1998; Thorson et al., 1998) or through second-hand information (Hedrick and Kortet, 2004; Lind et al., 2005). Predation risk is high while foraging (Krebs, 1980), as attention is likely divided between a minimum of two tasks (foraging and vigilance). Previous work shows that individuals mitigate predation threat by altering behaviour such as staying versus fleeing a foraging patch (Cresswell et al., 2003). This behaviour is decision making, but it is also arguably stimulus-response, rather than cognitive processing such as learning, memory or reversal learning. Indeed the effect of predation threat on the cognitive performance of individuals while foraging is largely unknown.

Distance and time

Every animal must contend with the extrinsic factors of space and time; in fact using spatial and temporal factors may help animals optimise their behaviour (Shettleworth, 2009). For example, nectar eating humming birds increase their foraging efficiency using episodic-like memory (what, when, where), when choosing when to return to previously rewarding flowers (Marshall et al., 2013). While there are numerous studies looking at the capabilities of animal spatial and temporal cognition (Healy and Hurly, 2004; Feeney et al., 2009), there has been little research into the effect that both

distance and time may have on other cognitive mechanisms. Distance is likely to affect many behaviours, such as territory holding, dispersal and foraging. For example, the relative distance between foraging sites may influence how well individuals learn, remember and update this information. Furthermore, food sources and site productivity change over time due to seasonal changes and fluctuation in prey items (Krebs and Davies, 1987), or density of conspecifics (Krebs, 1980). Therefore, animals need to mediate their behaviour according to external temporal cues, like light and temperature (Edery, 2000), or link their behaviour to a sequence of daily events (Richelle et al., 2013).

Finally, the effects of proximate factors can occur in concert. Using the previous example of alarm calls within a flock of foraging birds, the variation in how the birds react to this stimulus, may be a result of a number of intrinsic effects, such as hunger state (Duffield et al., 2015), previous experience (von Bayern et al., 2009), personality (Bell and Sih, 2007; Quinn et al., 2011) or distance to cover (Morand-Ferron and Quinn, 2011). Disentangling the effects of different proximate factors on performance of a cognitive trait requires carefully considered, validated tasks with the scope to separate out these effects. This is a complex, but necessary undertaking, if we are to further our understanding of individual differences in cognition and its evolution.

Paradigms for measuring cognitive variation

A plethora of tasks have been developed to tap into cognitive traits, where some tasks may involve several cognitive and non-cognitive traits, whereas others are more targeted towards a specific cognitive mechanism. Here I will discuss two extremes of each case: innovation and spatial learning, respectively. Innovation is defined as the generation of a novel behaviour or a known behaviour used in a novel context (Seed and Mayer, 2017) and is most commonly tested via extractive foraging problem solving tasks. Innovation helps animals find new food sources, or adapt to new environments (Lefebvre et al., 2004; Daniels et al., 2019) and correlates with relative brain size across species (Overington et al., 2009), suggesting an important role for cognitive mechanisms (Lefebvre et al., 1997; Reader and Laland, 2002; Sol et al., 2005; Benson-Amram et al., 2016). However, the definition of innovation is so broad that the scope of actions that meet the criteria is vast and contentious/questionable (Griffin and Guez, 2014). Despite the crucial role that innovation plays in acquiring

resources in changing environments, there remains two distinct problems. First, its usefulness as a measure of cognitive ability has been questioned because it is not possible to identify a specific cognitive mechanism that drives innovative behaviour (Rowe and Healy, 2014), particularly as motivation (Laland and Reader, 1999a), motor skills (Griffin and Guez, 2014), and personality (Dougherty and Guillette, 2018) have been shown to predict performance, and the extent to which these factors contribute to performance differs between studies. Secondly, the majority of experiments test for a binary measure of innovativeness, typically using extractive foraging problem solving device (Griffin and Guez, 2014; Seed and Mayer, 2017), where the animal must overcome a novel obstacle or perform a novel behaviour in order to reach a food reward. Reducing this composite behaviour down to a unitary trait (i.e. "innovativeness") masks the underlying nature of success, as the bulk of information regarding how they solved, for example through their persistence and accuracy is lost, traits that may be necessary to characterise when determining the causes and consequences of individual variation. To address the issue of what trait(s) is (are) important for determining innovation, testing for repeatability of different innovative measures (i.e. solve success, accuracy or persistence) would give insight into which trait(s) are consistent in determining innovation. Moreover, testing whether intrinsic and extrinsic factors affect innovation will help elucidate one or more of these factors driving consistent variation in performance. Therefore, by treating innovation as more than a binary measure and examining innovation in greater detail, we will have an opportunity to decipher the cognitive and non-cognitive mechanisms that may be involved in innovation.

In contrast to a latent variable such as innovation, spatial learning and memory are well-defined, related cognitive mechanisms that have been mapped to the hippocampus in humans and other animals (Maguire et al., 2000; Biegler et al., 2001), are enhanced in animals that rely on remembering spatial locations such as those that cache food (Pravosudov and Roth II, 2013), or rely on replenishing rates of food sources (Marshall et al., 2013), and in brood parasites that must remember locations of host nests (Guigueno et al., 2014). Evolutionary and ecological factors likely have enhanced spatial learning and memory, creating differences between species, sexes and individuals, depending on their specific needs. For example, for brood parasites such as the brown-headed cowbird, females have a large hippocampus and better

spatial memory than males, because they need to remember where they have previously laid eggs, so they don't eject their own potential offspring (Guigueno et al., 2014). Furthermore, spatial cognition is plastic and may vary between individuals of the same species, as evident in taxi driving humans (*Homo sapiens*), where the more use and reliance there is on spatial learning and memory, the larger the hippocampus is for that individual (Maguire et al., 2000). Although spatial learning and memory are well-defined cognitive mechanisms, measuring population variation in cognition may still be prone to the same challenges discussed above if individual performance is influenced by cognitive and non-cognitive factors. Therefore this thesis aims to investigate the extent to which proximate factors (intrinsic and extrinsic) contribute to performance across a range of different tasks that aim to measure innovation, spatial and temporal learning and memory, and reversal learning. Additionally, I will examine whether performance across these different cognitive tasks is repeatable, and if so, whether consistent individual differences in performance is driven by these proximate factors.

Study species

I used the great tit (*Parus major*) as the model organism for this thesis. The great tit is a cavity-nesting passerine bird, with a broad distribution ranging from Europe to Asia and North Africa (Gosler and Clement, 2007), where it occurs in a diverse range of habitats. It is the largest member of the Paridae family, weighing approximately 16g and males can be distinguished from females by the thicker black line of feathers running down their abdomen. The practical value of great tits as a model system stems from their tractability for experimentation, such as their use of garden feeders where they can be easily trapped and transported to an aviary. They are robust to living in aviaries where they participate in captive experiments and can be reared according to selection lines (Dingemanse et al., 2002). Experimental conditions in captive experiments can be tightly controlled, observed and measured, where the underlying causes of cognition can be monitored. However, experiments based in the wild are more informative with regards to the ecological factors that may drive individual differences in cognition. In terms of feasibility of study in the wild, great tits readily take to man-made nestboxes during the breeding season to raise their broods (Gosler, 1993). Furthermore, their movements and interactions can be tracked using non-invasive methods such as Passive Integrated Transponders (PIT) tags attached to their

leg, where visits to feeders as well as nestboxes can be monitored. Testament to the research effort devoted to the ecology of tits across Europe since the mid-20th century, there is a wealth of knowledge regarding the behaviour and ecology of great tits. The discovery of individual differences in cognition and personality displayed by great tits across a range of contexts is particularly relevant to my thesis, as I explore the influence of proximate factors (i.e. factors that may fluctuate daily or periodically) on cognition, and examine the extent to which this may influence the individual behaviour of great tits.

Thesis aims and structure

In this thesis, I investigated some of the understudied proximate factors that influence individual variation in innovation and cognition, in both the wild and captive settings. Firstly, I established whether motivation, inhibitory control or personality influence innovative problem-solving performance, and whether problem-solving performance is repeatable within individuals. Next, I examined whether diet and or fatty acids are linked to both personality and problem-solving. I then investigated the effect of perceived predation risk on learning performance to examine whether it could be an example of a non-lethal effect of predation. Lastly, I explored the effect of distance on spatial and temporal learning in wild mixed species flocks of great and blue tits, and whether there are any parallels between these learning abilities and behavioural flexibility.

My thesis is composed of four data chapters:

Chapter 2 investigates the influence of motivation, inhibitory control and personality on the behavioural processes that are predicted to cause variation during sequential innovative problem-solving, using second and third generation birds selected for personality. Adapting to environmental change is a major challenge faced by animals and the role of individual behavioural differences in facilitating this process is currently the focus of much research. Innovation, the generation of a novel behaviour or a known behaviour used in a novel context, is one form of behaviour that enables animals to respond to change. However, innovativeness is a composite trait driven by a range of disparate behavioural processes that selection may act on independently which explain consistent differences in performance among individuals. The objective of this chapter was to determine which factors and processes drive innovativeness and

explain the consistent individual differences observed. Here I used a multi-access problem solving device that incorporates three different extractive foraging techniques and used mixed models to understand the drivers of underlying variance components.

In **Chapter 3**, I explore the link between diet and fatty acid profiles on innovativeness and personality. As demonstrated in Chapter 2, food is a principal driver of variation in behaviour, as it is fundamental to survival and reproduction. However, very few studies have investigated the extent to which fatty acids are correlated or even influence behavioural variation in wild animals. To do so, I tested whether a seed diet or an insect diet differentially affected fatty acid profiles, and compared these profiles to those seen in their natural winter diet. I then investigated whether dietary manipulation and or, changes in fatty acid profile would change their exploration behaviour and problem-solving performance.

In **Chapter 4**, I examined the impact of personal and social perceived predation risk on spatial learning, behavioural flexibility and memory. Animals must navigate complex and fluctuating environments in order to forage successfully and therefore need to be proficient at switching between searching, learning and returning to food sources, while simultaneously remaining vigilant for predators. Spatial learning facilitates these foraging processes, however the effect of predation risk on spatial learning and cognition remains unknown. I hypothesised that varying levels of predation risk would influence learning speed, behavioural flexibility and memory in a foraging task.

Lastly, in **Chapter 5**, I explored the effect of distance on spatial and temporal learning in wild mixed species flocks. Foraging is an energetically and cognitively demanding activity, because not only do animals have to search for food, they must also learn and remember when and where to find it, and to update this information as foraging patches change. However, to date little research has examined how both spatial and temporal information influence foraging efficiency through cognitive processes in the wild. In this final data chapter, I examined whether the distance between feeders and the time of day that they were rewarding influenced performance and individual consistency across different measures of cognition, namely discrimination learning, memory, temporal learning and reversal learning.

Additional research

In addition to the chapters enclosed in this thesis, I have also been involved in the following research during my studies:

Davidson Gabrielle L., Cooke Amy C., Johnson Crystal N. and Quinn John L. (2018) The gut microbiome as a driver of individual variation in cognition and functional behaviour. Philosophical Transactions of the Royal Society B. **373**20170286

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Troisi Camille A., Cooke Amy C., Davidson Gabreille L., de la Hera Ivan, Reichert Michael S., Quinn John L. (2021) No evidence for cross-contextual consistency in spatial cognition and behavioural flexibility in a passerine. Animal Behavior and Cognition, 8(3), 446-461.

Chapter 2. Motivation, accuracy and positive feedback through experience explain innovative problem solving and its repeatability

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Contributions: ACC GLD and JLQ designed the study. ACC and GLD collected the data. ACC conducted statistical analysis and led the manuscript writing. All authors contributed to interpretation of results and revisions of the manuscript.

Abstract

Adapting to environmental change is a major challenge faced by animals and the role of individual behavioural differences in facilitating this process is currently the focus of much research. Innovation, the generation of a novel behaviour or use of a known behaviour in a novel context, is one form of behaviour that enables animals to respond to change. By deciphering the mechanisms underlying innovativeness, especially those that explain consistent differences between individuals, we can further understand the consequences of this behavioural variation. I tested whether

motivation, experience, inhibitory control and personality were linked to different stages of sequential innovative problem-solving performance among great tits, *Parus major*, and of their overall innovativeness across tasks. I gave animals originating from lines bidirectionally selected for fast or slow early exploratory behaviour, a multiaccess problem-solving device. Diverse motor skills and behavioural flexibility were required to solve all three different access points sequentially over trials. Food-deprived, highly motivated birds had shorter latency to touch the device, were more likely to solve an access point within a trial, and solved a greater diversity of them, than their less motivated counterparts. Solving success increased with accuracy when interacting with the device (proportion of touches to functional components of the device compared to all touches to the device per trial), and with previous experience. Personality selection lines and inhibitory control had little effect. Repeatability analysis showed that between-individual differences in problem-solving performance were explained by: (1) pseudorepeatable effects (upward bias) linked to hunger-induced motivation, (2) repeatable differences in accuracy when interacting with devices, and (3) a feedback loop caused by experience gained over successive trials. My results highlight the challenges of characterizing consistent individual variation in behaviour generally and support the idea that complex sources of variation play an important role in problem-solving performance.

Keywords: accuracy, cognitive repeatability, inhibitory control, innovation, motivation, *Parus major,* personality, problem solving, pseudorepeatability

Introduction

Acquiring resources in changing environments is a major challenge faced by animals and a key determinant of fitness. Innovation, the generation of a novel behaviour or use of a known behaviour in a novel context, most commonly achieved through a problem-solving process, is one mechanism that a wide range of animals use to meet this challenge (Seed and Mayer, 2017). Comparative analysis has provided evidence for selection acting on innovativeness across species, because it helps animals find new food sources, or adapt to new environments and seasonal changes (Webster and Lefebvre, 2001; Reader and Laland, 2002; Reader, 2003; Lefebvre et al., 2004; Sol et al., 2005; Daniels et al., 2019). Furthermore there is growing evidence of a link between innovativeness and fitness within populations (Cole et al., 2012; Cauchard et

al., 2013; Preiszner et al., 2017), and that innovation enables invasive or urbanized species to make use of novel resources (Griffin et al., 2014; Griffin and Diquelou, 2015; Daniels et al., 2019). Although the underlying proximate causes of individual variation in innovativeness are diverse (for example, infection by parasites, (Dunn et al., 2011); social factors, (Thornton and Samson, 2012); natal environment effects, (Kotrschal and Taborsky, 2010)), repeatability analyses suggest differences between individuals are consistent, pointing to intrinsic, potentially additive genetic, sources of variation (Cole et al., 2011; Morand-Ferron et al., 2011; Cauchoix et al., 2018). One of the major challenges in the field is that innovativeness is a composite trait driven by a range of disparate behavioural processes that selection may act on independently and that may explain consistent differences in performance between individuals. These processes include cognition and motivation, as well as personality traits like exploration, persistence and neophobia (Taylor et al., 2009; Seed and Call, 2010; Griffin and Guez, 2014; Lermite et al., 2017). Thus, a key objective is to determine which processes drive innovativeness and explain the consistent individual differences observed.

Innovativeness correlates with relative brain size across species (Overington et al., 2009), suggesting an important role for cognitive mechanisms (Lefebvre et al., 1997; Reader and Laland, 2002; Sol et al., 2005; Benson-Amram et al., 2016). A number of cognitive mechanisms have been proposed to underlie innovative problem solving, including causal reasoning, insight, associative learning and inhibitory control (Benson-Amram and Holekamp, 2012; Barrett et al., 2018). Additionally, the ability to draw on previous experience aids individuals in reaching a solution (Sol et al., 2012; Cauchard et al., 2013; Griffin et al., 2014; Ebel and Call, 2018), as well as ensuring that the new behaviour becomes established in an individual's repertoire (Fragaszy et al., 2013). Finally, in situations where opportunities for innovation may be common, for example among invasive or urbanized species (Griffin et al., 2014; Griffin and Diquelou, 2015; Daniels et al., 2019), the ability to innovate frequently may be essential but dependent on inhibitory control (Daniels et al., 2019), whereby individuals must inhibit a previously rewarding behaviour that is no longer rewarding, in order to innovate further (Pecora et al., 2017). However, cognitive processes alone cannot explain why some individuals innovate more than others (van Horik and Madden, 2016), and especially when other behavioural traits such as exploration and

persistence also lead to innovation (Overington et al., 2011; Ebel and Call, 2018; Daniels et al., 2019).

Personality, defined as within-individual behavioural consistency across time and contexts (Réale et al., 2007), provides a framework for exploring constraints on behavioural plasticity (Dall et al., 2004) and individual problem-solving performance (Morton et al., 2013; Hopper et al., 2014). Personality traits have attracted particular attention because they predict individual variation in a wide range of behavioural traits (Cole and Quinn, 2012, 2014; Aplin et al., 2014). Studies in the wild (Dingemanse et al., 2002; Highcock and Carter, 2014) and in the laboratory (David et al., 2012; van Oers and Naguib, 2013) show that the personality trait 'early-life exploratory behaviour' (more specifically in this case, repeatable differences in the reaction to both a novel environment and objects (Drent et al., 2003)) can influence how individuals retrieve information from their environment (Smit and van Oers, 2019), how quickly they solve problems (Hopper et al., 2014), and the degree of behavioural flexibility shown (Coppens et al., 2010). In particular, fast-exploring (hereafter 'fast') individuals may be quicker to interact with or solve tasks (Benson-Amram and Holekamp, 2012; Trompf and Brown, 2014) but show less behavioural plasticity (Amy et al., 2012; Logan, 2016a; Jolles et al., 2019). Slow-exploring (hereafter 'slow') individuals tend to be the opposite (Coppens et al., 2010; Sol et al., 2012; Ducatez et al., 2015a; Zandberg et al., 2017; Johnson-Ulrich et al., 2018). Additionally, neophobia (the fear of novel food, objects or places (Greenberg and Mettke-Hofmann, 2001)) can constrain both the latency to approach a novel object and engagement in tasks. For example, individual hyenas, *Crocuta crocuta*, that showed greater persistence, activity or lower neophobia were faster to solve a problem (Johnson-Ulrich et al., 2018). However, the evolutionary significance of links between innovation and personality traits, as defined in Réale et al. (2007), is often unclear because the genetic basis for the personality variation is usually unknown (Cole et al., 2011), except in those few cases involving great tits (*Parus major*) where personality-selective breeding lines have been used (Drent et al., 2003; van Oers et al., 2004, 2005). Moreover, the role of other personality traits at different stages of innovative problem solving (e.g. interacting with a problem, solving a problem and ceasing to perform outdated solutions) and its interactions with other factors such as stress and motivation remain largely unexplored. Individual differences may be especially pronounced under stress

(Suomi, 2004), but this has scarcely been tested. Note that although all behavioural variation can be defined as personality in a statistical sense (e.g. Dingemanse & Dochtermann, 2013), here I follow Réale et al. (2007) who focused on five kinds of behavioural traits, including exploration behaviour, that inherently capture variation in many other behavioural traits.

Motivation is expected to be an important driver of innovative behaviour (Laland and Reader, 1999a; Sol et al., 2012) and to affect all stages of innovation. The 'necessity drives innovation' hypothesis states that innovative behaviours commonly occur when individuals are in need (Reader and Laland, 2003), that is, when they are motivated (Laland and Reader, 1999a). For example, subdominant or juvenile individuals are often assumed to be more likely to innovate because they are less competitive when foraging (Morand-Ferron et al., 2011; Thornton and Samson, 2012). The rarely tested assumption in these studies is that hunger acts as the motivating factor driving innovation. In animal behaviour studies, food deprivation is commonly applied to ensure trial participation (Birch, 1945; Overington et al., 2011; Sol et al., 2012), or when attempting to control for confounding effects of motivation (Ebel and Call, 2018; van Horik and Madden, 2016). However, the extent to which motivation may influence innovative problem-solving behaviour at an individual level has scarcely been examined explicitly (Griffin & Guez, 2014).

Here I explore behavioural processes that are predicted to cause variation during sequential innovative problem solving, using second- and third-generation birds selected for personality. Selection lines are a powerful means to investigate inherent effects of personality on problem-solving performance as opposed to simple phenotype–phenotype correlations. I used a device that incorporated three different extractive foraging access points to provide a more complete measure of individual performance. The solutions relied on different motor skills, thus limiting the effects of individual motor skill bias, and previous motor skill experience carrying over to solving new access points. I examined variation in three different behavioural assays involved in innovative problem solving: (1) latency to touch the novel apparatus; (2) accuracy when interacting with any access point on the device; (3) problem-solving success within each trial. Then I examined (4) the individual's overall innovativeness (the number of different access points solved at least once across all trials). I considered a range of potential explanatory factors for these different behavioural

facets, including extrinsic motivation (hunger state, the only experimentally manipulated factor), inhibitory control, previous experience and personality (fast/slow selection lines). In line with the theory that individual differences may be more pronounced under stress (Suomi, 2004), I investigated the interaction between motivation and personality, assuming that birds in the high-motivation (food-deprived) treatment were more stressed than those in the low-motivation treatment. Finally, to determine whether individual differences were consistent, I estimated repeatability for (1)–(3) and examined whether controlling for fixed effects modified my estimates of repeatability. Repeatability sets the upper limit of heritability and is fundamental in studies on the evolutionary ecology of innovation and behaviour generally. Although uncontrolled confounding effects can potentially lead to an underestimate of repeatability, more commonly they lead to overestimates (pseudorepeatability) and sometimes explain repeatability entirely (Catry et al., 1999; Westneat et al., 2011; Dingemanse and Dochtermann, 2013).

I predicted that: (1) birds in the high-motivation treatment group would have a reduced latency to touch the device, show increased accuracy (i.e. a high proportion of interactions with functional components, rather than nonfunctional components of the device), be more likely to solve an access point and solve more of them; (2) fast explorers would have a shorter latency to touch the device and lower accuracy when interacting with the device than slow explorers, but they may have a higher likelihood of solving due to higher exploration of the device; (3) previous experience would enable innovation, by causing a decrease in latency to touch the device, an increase in accuracy when interacting with it, and an increased likelihood of solving; (4) likelihood of solving in a trial would increase with accuracy (i.e. with higher frequency of interactions with functional components); and (5) birds with higher inhibition ability would be more likely to adjust their behaviour to solve multiple access points.

Methods

All experiments were carried out at the Netherlands Institute of Ecology (NIOO-KNAW), on 36 captive-bred great tits, *Parus major*. All birds included in the study were adult (2 years or older). Seventeen birds were not related to each other, five had one sibling and 14 shared more than one sibling; I assume relatedness between individuals had no bearing on the results. They were housed individually in standard

cages (0.9 × 0.5 m and 0.5 m high) containing three perches and a water bath. Birds were in auditory contact but were visually isolated to prevent social learning. All birds had ad libitum access to water and a maintenance diet (ground beef heart, commercial egg food, fruit and calcium) unless otherwise stated. One bird did not participate in any of the experiments and was thus excluded from any analysis.

Personality

Birds came from the second and third generation of bidirectionally phenotypically selected great tits, based on personality for 'fast exploration' (fast, $N = 18$) and 'slow exploration' (slow, $N = 18$). The measure of 'exploration' used during the selection process was a combination of two novel object tests where the latency to touch a novel object was recorded (e.g. a pink panther toy or an AA battery taped to a wooden stick), and one novel environment test where birds were released into a room and the latency to land on the fourth out of five artificial trees was recorded (for further details on selection and personality lines see Drent et al., 2003). The birds in the final selection lines used here underwent these same assays after fledging to confirm their personality type. As the specific aim of this study was to investigate the effects of artificially selected personality lines on problem solving and because the bird behaviour matched their selected personality type, I analysed personality according to their selection history only (i.e. fast or slow selection lines).

Motivation

Individuals were randomly assigned to one of two motivation treatment groups for the duration of the experiment based on hunger state. The low-motivation group consisted of sated individuals, given full access to maintenance diet up to the start of the trial. Additionally, to ensure that they were sated, they were given three wax moth, *Achroia grisella*, larvae 30 min before trials began, and invariably ate them all. The high-motivation group consisted of food-deprived birds, which had all sources of food removed from their cage for 1 h before the trial (Hämäläinen et al., 2019). For welfare purposes, all birds had access to water during the trials. Motivation treatment was spread across the selection lines in four categories: high motivation, fast (female $N = 4$ and male $N = 5$); high motivation, slow (female $N = 5$ and male $N = 4$); low motivation, fast (female $N = 5$ and male $N = 4$); low motivation, slow (female $N = 5$ and male $N = 3$).

Lever-pulling Propensity

All trials described here and in the following section were carried out in the birds' individual home cages, under natural winter diurnal light cycles. To establish whether the birds had a pre-existing tendency to lever pull (von Bayern et al., 2009), and because some birds may have had previous experience lever pulling in previous experiments while others had not, I measured lever-pulling propensity prior to testing them on the multiaccess device. I presented all birds with an opaque PVC rectangular tube containing a lever-supported platform with half a wax moth larva (Zandberg et al., 2017). I used an opaque device to test whether birds had a propensity to pull a stick, independent of a visual food reward cue, because the previous device that had been used was also opaque (Zandberg et al., 2017), and because I did not want the birds to have experience with the main innovation test device beforehand. All birds were given up to four trials (30 min per trial) to obtain the food reward, by pulling the lever horizontally causing the platform and reward to drop. Individuals that solved this opaque task at least once were classified, in the main analysis on the multiaccess problem-solving task described below, as having previous experience with solving the lever-pulling task. All birds progressed to the multiaccess task irrespective of their performance in this opaque device (Fig. 1).

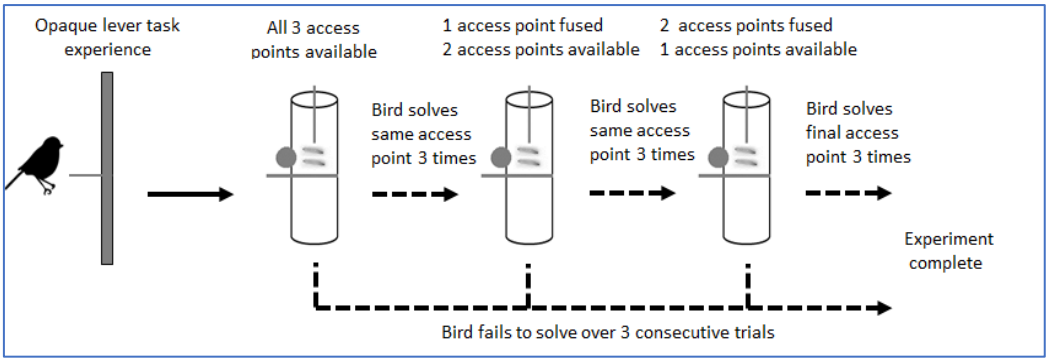

Figure 1. Routes of progression through the multiaccess problem-solving experiment. To quantify their previous experience and propensity to pull sticks, individuals were initially presented with an opaque tube with a lever. They had four trials (30 min each) in which to pull the lever. Once they solved the task once, they were classified as having previous experience solving a lever task. All birds progressed to the multiaccess problem-solving task where they were presented with the transparent experimental device in which three access points were functional. Each bird had to solve the task using the same access point three times, before moving onto the next phase, where the previously solved access point was fused, leaving the remaining functional access points. This process was repeated for the other two access points. At any point of the testing, if a bird failed over three consecutive trials, its participation in the experiment ended. Dashed arrows indicate there is an alternative progression to complete the experiment.

Multiaccess Problem-Solving Task

Birds were presented with a multiaccess problem-solving apparatus (Fig. 2) with three distinct solutions that required different motor skills (see below), to obtain a preferred food reward (a wax moth larva). The apparatus was an upright Perspex cylinder (5 cm diameter and 16 cm high), with a platform holding the food reward. The platform was supported by a lever, which when pulled from the outside of the device caused the platform to drop, releasing the food reward below the device (solution 1). A second possible solution was to move a door that could be pushed left or right, to gain access to the food reward on the platform (solution 2). A third possible solution was to pull a string from the top of the device, which was attached to a second larva (solution 3). Each of these access points involved different motor action(s) including pulling

(solution 1), pushing (solution 2) and coordinating both grasping and pulling (solution 3).

Experiments were scheduled evenly across mornings and afternoons for both treatments and personality lines. In each trial, subjects were presented with the device and given 30 min to solve any of the access points. Birds were given two trials per day, back-to-back, without being fed between trials. Following their second trial, their maintenance diet was returned until testing the following day. The experiment ended when they had solved all three access points three times, or when they had failed to solve any over three consecutive trials (total number of trials 3–13). Once an individual solved the same access point across three separate trials, that access point (door, lever or string) was fused, mimicking natural depletion of that food source, which meant that solving that access point was no longer possible, although it remained present and visible. I allowed birds to solve each access point three times to increase the chance that the behaviour became fixed in their repertoire. To solve a novel solution, they would need to behave flexibly, which I predicted would be guided by inhibitory control. Great tits from selection lines in this facility readily participate in experiments, so I assumed the three trials were sufficient to allow them to overcome any neophobic response.

All trials were recorded using a Panasonic HC-V250EB-K camera mounted on a tripod, covered in camouflage tape and positioned 1 m from the cage. Videos were analysed using Behavioural Observation Research Interactive Software (BORIS;(Friard and Gamba, 2016). Observers were blind to the personality assigned to the birds but were aware of the motivation treatment group. Ten per cent of videos were coded by a second person. Interrater reliability was assessed using a Kendall's tau correlation test for agreement on the following measures: total number of touches to the device per trial, $P < 0.001$; touches to functional access points on the device per trial, $P < 0.01$; touches to anything other than functional access points on the device per trial, $P < 0.005$.

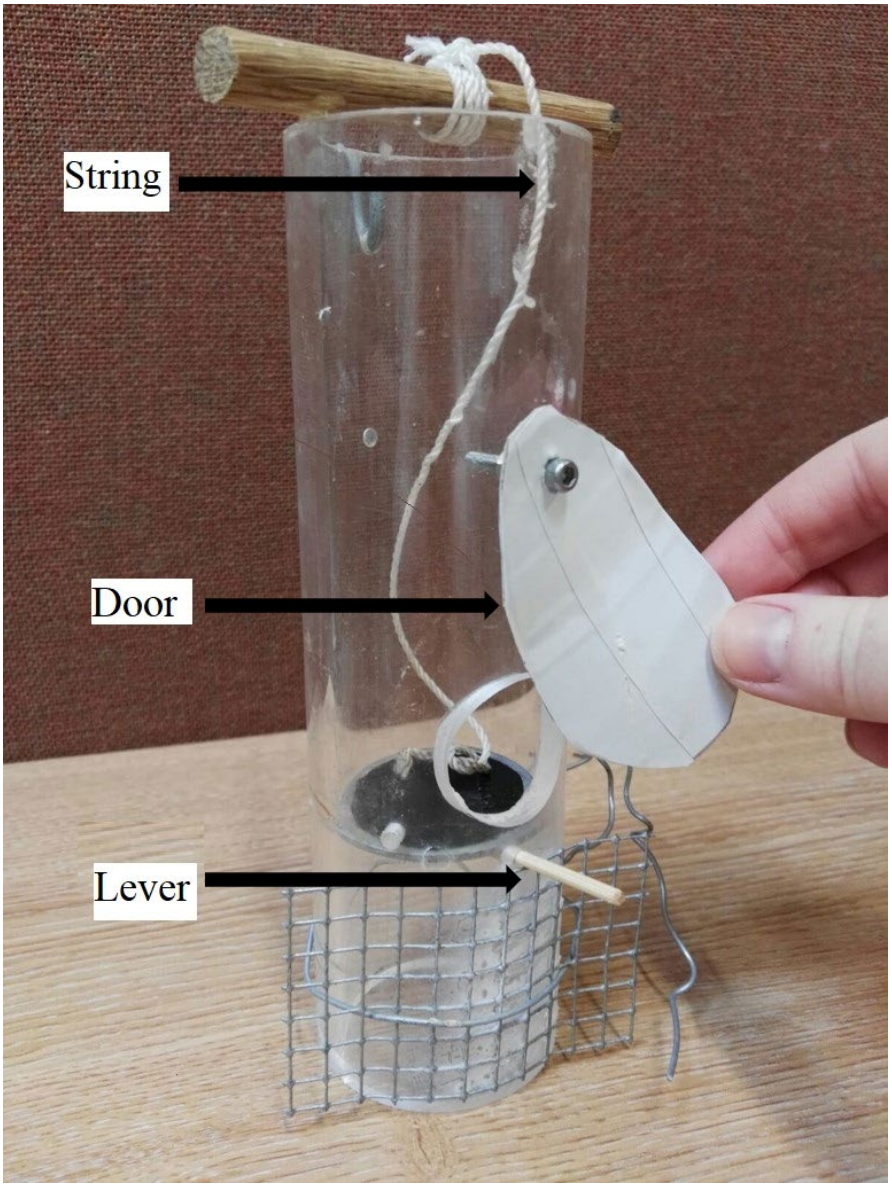

Figure 2. The multiaccess problem-solving device given to birds in their home cage. The apparatus has three different access types to retrieve the food reward inside: a lever, a swing door, and a string.

Inhibition Task

To generate an independent estimate of each individual's motor inhibition, I used a classical detour-reaching task (Rothbart et al., 1985; Boogert et al., 2011; Beran, 2015), which tests to what extent the birds could control the prepotent response of pecking straight towards a food reward visible within a transparent Perspex tube. To pass the test, birds had to obtain the reward by accessing it through the opening on the side (Thorndike, 1911). The detour task was performed on a subset of 20 birds, prior

to the problem-solving task (number of days between end of the detour-reaching task and first test day on the multiaccess device: mean ± SE = 11 ± 0.46, minimum = 8, maximum = 12) to control for carryover experience with the transparent Perspex. Birds were not food deprived before this task. There were three phases to this task: habituation, training and test phases. Birds participated in one phase per day, with progression through the phases occurring over consecutive days (duration of testing: mean ± SE = 1.64 ± 0.18 days, minimum = 1, maximum = 4). In the habituation and training phases, the Perspex tube was opaque (covered with black tape). To familiarize the birds with the apparatus, a wax moth larva was placed at the opening edge of the tube. Birds passed the habituation phase when they had eaten the reward three consecutive times. During the training phase, individuals had to obtain the food reward located in the centre of the opaque tube without touching any other part of the device. Training was completed when this was done successfully during four of five consecutive trials, ensuring the birds had the motor skills and experience necessary to move around the tube to successfully obtain the larva. During the test phase, the food reward was placed in the centre of a transparent tube. Birds had to remove the food reward without pecking on any other part of the device to complete the trial successfully. Inhibitory control scores were quantified as the number of trials it took individuals to complete four of five consecutive trials correctly. All trials were a maximum of 3 min each and observed remotely by livestreaming to a mobile phone using a Wi-Fi-enabled SJCAM SJ4000 camera (Shenzhen Zhencheng Technology, Shenzhen, China).

Ethical Note

I performed the experiment in accordance with the ASAB/ABS guidelines. All experiments were approved by an ethical committee (DEC-KNAW licence no. NIOO 14.12 to K.V.O.) and daily health checks were carried out to ensure the birds' welfare. Birds were returned to the stock population after the experiment.

Statistical Analysis

I tested whether multiple factors influenced different behaviours at different stages of sequential innovative problem-solving performance: (1) latency to touch, (2) accuracy, (3) likelihood of solving and (4) innovativeness. Separate analyses were conducted using R Studio (RStudio Team, 2019) on each of the four phases described

above (1–4), and I repeated these models on the subset of birds (N = 22) that completed the inhibition task. For touch latency and accuracy, I conducted general linear mixed models (GLMMs) using the nlme package (Pinheiro et al., 2019) fitted with a normal distribution; for likelihood of solving I ran a GLMM using the lme4 package (Bates et al., 2015) fitted with a binomial distribution; and for innovativeness I ran a general linear model (GLM) with Poisson distribution (see Table A1 for a full list of variables and their definitions). In line with Whittingham et al. (2006), I retained all variables of biological significance in the initial models to test specific hypotheses. For model selection, I used Akaike's information criterion (AIC) to measure goodness of fit (reported in table legends) and likelihood ratio tests to determine which model explained more variance. I compared full models (with the interaction between motivation and personality) to null models, and then compared full models to reduced models (i.e. without the interaction between motivation and personality). I dropped the interaction term from the model if the likelihood ratio test was nonsignificant (alpha = 0.05). To confirm that this hypothesis testing approach did not lead to a Type 2 error due to overfitting, I further reduced each model to the minimum adequate model using backwards reduction (see Tables A2–A5). I checked that all models met assumptions (homogeneity, normality of residuals and collinearity of explanatory variables) using the DHARMa package in R (Hartig, 2020). I calculated confidence intervals (CI) for the random factor and residuals in each model using the package nlme in R (Pinheiro and Bates, 2006). In the legend of each table, I report marginal R^2 (defined as the proportion of variance in the dependent variable that is explained by the fixed factors only), and conditional R^2 (defined as the proportion of variance in the dependent variable that is explained by the fixed and random factors), or pseudo R^2 (the marginal R^2 of a Poisson GLM, which does not include random factors). I tested the following full models.

Latency to touch the device was log transformed to fit a Gaussian distribution (total trials = 226). The following fixed effects were included in my model: motivation (low or high), trial number, selected personality lines (fast or slow exploring), previous experience of solving any functioning access point including the opaque device (no or yes) and sex (male or female). Individual bird identity was included as a random effect to control for repeated measures and to test repeatability of individual differences.

Accuracy was defined as the number of touches to a functioning access point divided by the total number of touches to any part of the device per trial. Fixed effects included interaction rate (total number of touches to any part of the device per min, per trial), motivation group, trial number, selected personality lines, previous experience of any functioning (but not fused) access point (including previous experience of lever-pulling propensity on opaque device), fused trial (where any of the solutions were fused and therefore unavailable, as a fused access point may decrease accuracy) and sex. Individual bird identity was included as a random effect as subjects completed multiple trials.

To test which factors predicted solving within each trial (binary; $N = 224$), I included the following fixed effects: accuracy, previous experience, motivation group, personality, sex, trial number and fused trial. Individual bird identity was included as a random term. To limit overparameterization in the model, I did not include latency to touch in this analysis (but see analysis on number of different solves).

I tested which factors affected innovativeness defined as the number of different access points solved by an individual ($N = 35$). Birds solved either 0, 1, 2 or 3 different access points. I included the following explanatory variables: hunger, personality, sex, latency to touch the device in the first trial only and inhibitory control. As this analysis was conducted on the number of different access points solved across all trials, I did not include variables that are trial specific (i.e. previous experience and accuracy).

Finally, I determined individual repeatability of the response variables in each of the first three questions above (latency to touch the device, accuracy and solving within a trial), using the rptR package, estimating repeatability (intraclass correlation) and CIs from Gaussian, binary, proportion and Poisson data (Stoffel et al., 2017). I report unadjusted and adjusted repeatability, to encompass repeatability before and after controlling for influential fixed effects (Cauchoix et al., 2018). Unadjusted repeatability measures the between-individual variation in a given behaviour, while adjusted repeatability controls for fixed effects that could influence individual behaviour, because they explain either between- or within-individual components of variation. For both adjusted and unadjusted repeatability, I included individual identity as a random effect. Data and R code are included in the supplementary material.

Results

Latency to Touch the Multiaccess Device

Latency to touch the multiaccess device decreased over consecutive trials (Table 1, Fig. A1). The high-motivation group took less time to touch the device than the low-motivation group. Latency to touch the device did not differ between the personality selection lines. There was a nonsignificant trend for sex, suggesting that males took less time to touch the device than females. The variance of the random effect (individual bird identity) and the residual are indicated in Table 1. There was no effect of previous experience. The interaction between motivation and personality was not significant (β ± SE = –0.47 ± 0.60, t = –0.78, P = 0.44). Inhibitory score had no effect on latency to touch the device (see Table A6).

Table 1 Full model outputs from GLMM with factors effecting latency to touch the device per trial

Fixed effects	β ± SE	t	P
Intercept	4.27 ± 0.35	12.69	<0.001
Motivation group [a]	**1.17 ± 0.30**	**3.84**	**<0.001**
Personality [b]	0.20 ± 0.30	0.67	0.504
Trial number	**–0.09 ± 0.03**	**–3.36**	**0.001**
Sex [c]	–0.53 ± 0.30	–1.76	0.089
Previous experience [d]	–0.19 ± 0.17	–1.15	0.25

N = 226, df = 190, R^2 (marginal = 0.26, conditional = 0.49, AIC = 739.83). Random effect included bird identity (0.72; 95% confidence interval, CI = 0.51, 1.02) and the residual variance (1.08; 95% CI = 0.97, 1.19). Significant results (P < 0.05) are highlighted in bold. [a] Low (reference level is high). [b] Slow (reference level is fast). [c] Male (reference level is female). [d] Yes (reference level is no).

Accuracy

Birds were more accurate if they had previous experience solving any functioning access point, including solving the opaque device before the main experiment (Table 2, Fig. 3). There was a nonsignificant trend for slow birds being more accurate than fast birds. Birds tended to be less accurate in trials where there was a fused access point. The variance of the random effect (individual bird identity) and residual are indicated in Table 2. There was no effect of motivation group, interaction rate, sex or trial number on accuracy. The interaction between motivation and personality was not significant (β ± SE = –0.06 ± 0.15, t = –0.39, P = 0.70). Inhibition was unrelated to accuracy (see Table A7).

Table 2 Full model outputs from GLMM with factors affecting accuracy per trial

Fixed	β ± SE	t	P
Intercept	0.29 ± 0.08	3.44	<0.001
Interaction rate	0.00 ± 0.00	0.43	0.670
Previous experience [a]	**0.35 ± 0.04**	**8.20**	**<0.001**
Personality [b]	0.13 ± 0.07	1.80	0.082
Motivation group [c]	–0.04 ± 0.07	–0.54	0.591
Fused trial	–0.11 ± 0.07	–1.70	0.091
Sex	0.05 ± 0.07	0.64	0.524
Trial number	–0.00 ± 0.00	–0.33	0.744

N = 222, df= 182, R^2 (marginal = 0.33, conditional = 0.56, AIC = 209.4). Random effect included bird identity (0.24; 95% confidence interval, CI = 0.22, 0.27) and the residual variance (0.15; 95% CI = 0.10, 0.23). Significant result (P < 0.05) is highlighted in bold. [a] Yes (reference level is no). [b] Slow (reference level is fast). [c] Low (reference level high).

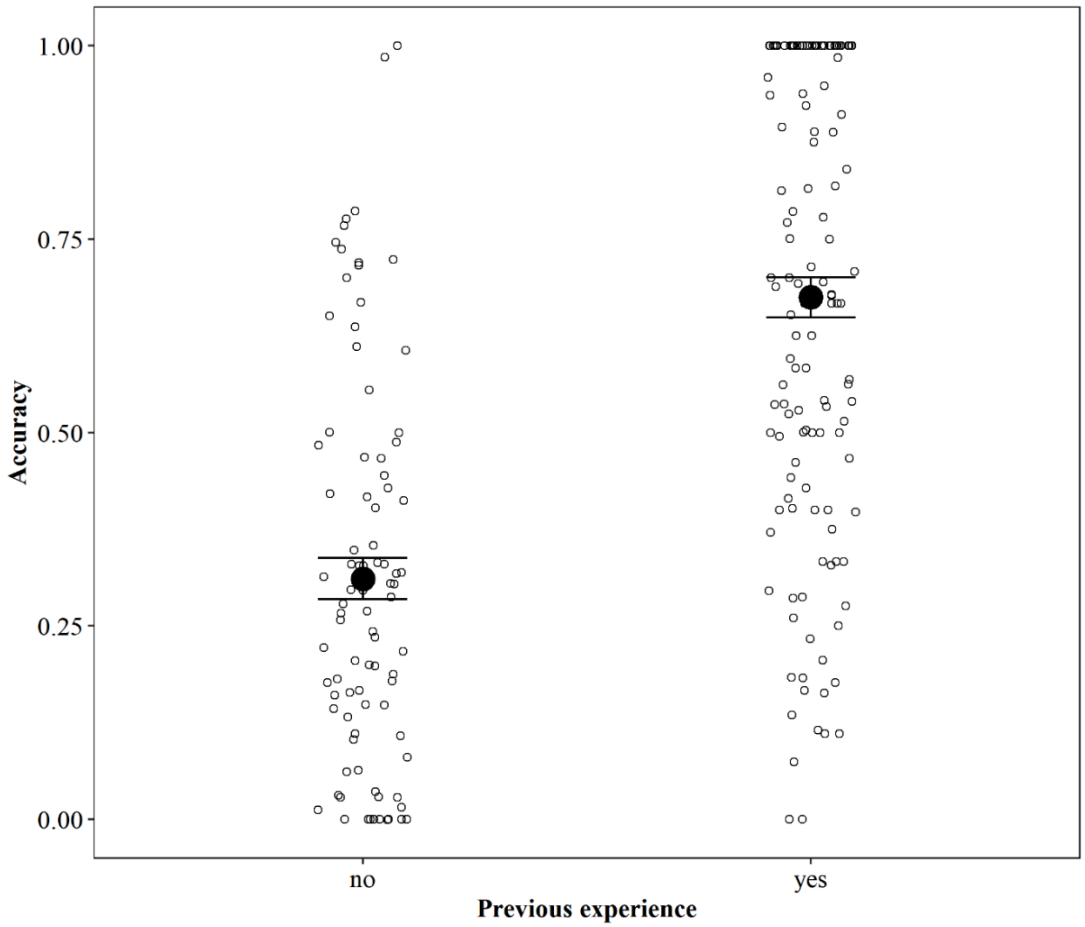

Figure 3. The effect of previous experience (whether there was an access point available that the bird had solved previously including the opaque device) on accuracy (the number of touches to functional parts of the device divided by all touches to the device per trial; see Table 2). Note that a previously solved access point could still be available as birds had to solve each access point three times before it was fused, thus making it unavailable. Smaller points represent individual birds (which have been jittered along the X axis to reduce overlap; as a result, any remaining overlap results in darker points). The large point represents the mean and the error bars represent SEs.

Solving Within a Trial

Nineteen of the 35 birds pulled the lever on the opaque device. Of the 35 birds that participated in the multiaccess task, 12 solved one access point, four solved two access points, seven solved all three access points and 12 did not solve any (Fig. 4). Three birds solved three different access points over three consecutive trials while the device was fully operational (all access points functioning). One bird solved two access points

in one trial, solving the string and then the lever in their fourth trial. I include both solutions as separate observations in my analysis. The lever was solved by 23 different birds, the door was solved by 10 birds and the string by seven birds, while 12 birds did not solve any access point.

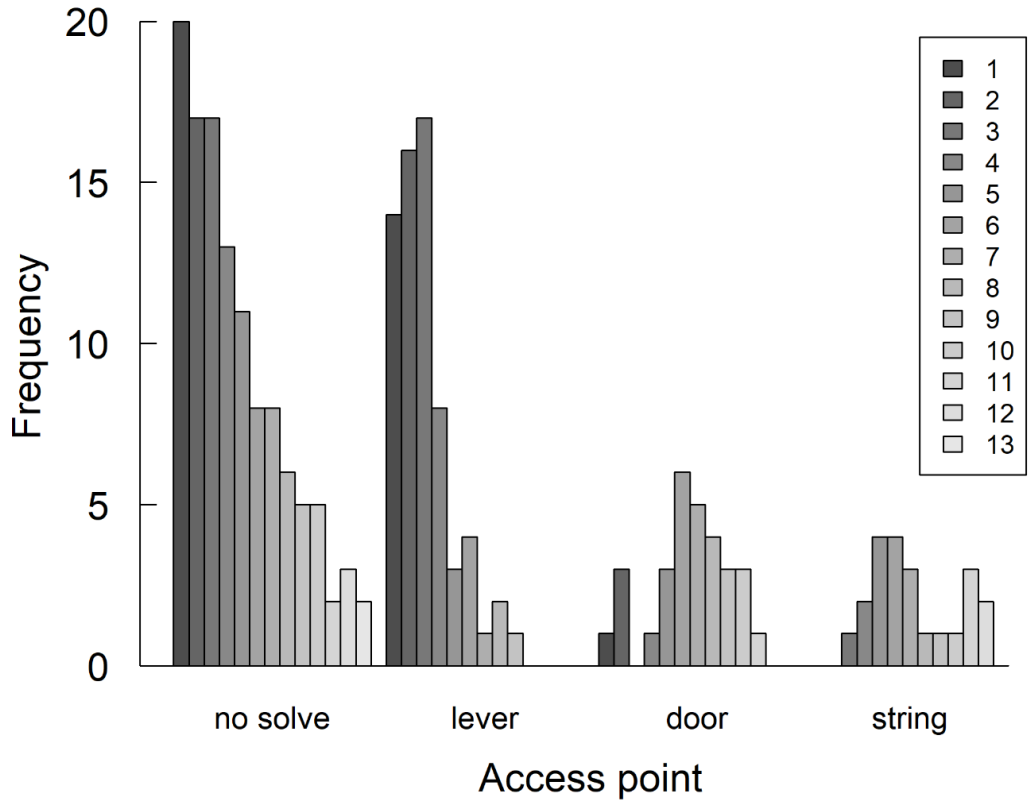

Figure 4. The frequency of access points solved, grouped by type of access point solved in each trial where each column refers to the trial number where the solve occurred.

Food-deprived birds were more likely to solve an access point (Table 3). Higher accuracy and previous experience also predicted solving likelihood within a trial. The variance of the individual identity random effect and the residual are indicated in Table 3. There was no effect of personality, sex, trial number, whether it was a fused trial or not, total number of touches to device per trial or inhibition (see Table A8). The interaction between motivation and personality was not significant ($\beta \pm SE = -0.46 \pm 0.90$, $t = -0.51$, $P = 0.61$). Follow-up post hoc analysis, using a Fisher's exact test,

revealed a correlation trend between lever pulling on the opaque and multiaccess device ($P = 0.07$). Further analysis, investigating the order in which the multiaccess device was solved, using a Fisher's exact test, showed that the lever was more likely to be solved first ($P < 0.001$), while there was no difference between the string or door. Fig. 4.

Table 3 Full model outputs from GLMM with factors affecting solving within trials

Fixed effects	β ± SE	*z*	*P*
Intercept	–1.93 ± 0.68	2.86	0.004
Accuracy	**3.79 ± 0.78**	**4.90**	**<0.001**
Previous experience [a]	**1.26 ± 0.47**	**2.66**	**0.008**
Motivation group [b]	**–1.79 ± 0.50**	**–3.57**	**<0.001**
Personality [c]	–0.68 ± 0.43	–1.58	0.115
Sex [d]	0.26 ± 0.43	0.61	0.541
Trial number	0.09 ± 0.10	0.85	0.395
Fused trial [e]	–0.18 ± 0.73	–0.25	0.806
Total number of touches per trial	–0.00 ± 0.00	–1.47	0.141

$N = 224$, $df = 216$, R^2 (marginal = 0.51, conditional = 0.52, AIC = 55.85). Random effect included bird identity (0.37; 95% confidence interval, CI = 0.41, 0.33) and the residual variance (0.13; 95% CI = 0.10, 0.27). Significant results ($P < 0.05$) are highlighted in bold. [a] Yes (reference level is no). [b] Low (reference level is high). [c] Slow (reference level is fast). [d] Male (reference level is female). [e] Yes (reference level is no).

Innovativeness: Number of Access Points Solved

Highly motivated birds solved more novel access points than little-motivated birds (Table 4, Fig. 5). There was no effect of personality, sex, latency to touch the device in the first trial only (Table 4) or inhibition (Table A9). The interaction between personality and motivation was nonsignificant (β ± SE = –0.86 ± 0.79, $z = –1.09$, $P = 0.28$).

Table 4 Full model outputs from GLM with factors affecting the number of different access points solved by an individual

Explanatory variables	β ± SE	*z*	*P*
Intercept	<0.001 ± <0.001	1.84	0.066
Motivation group [a]	**–1.04 ± 0.37**	**–2.80**	**0.005**
Personality [b]	–0.01 ± 0.032	–0.30	0.761
Sex [c]	0.18 ± 0.32	0.57	0.567
Latency to touch the device (in first trial only)	<0.001 ± <0.001	–0.35	0.727

N = 35, df = 24, pseudo-R^2 = 0.24, AIC = 99.60. Significant result ($P < 0.05$) is highlighted in bold. [a] Low (reference level is high). [b] Slow (reference level is fast). [c] Male (reference level is female).

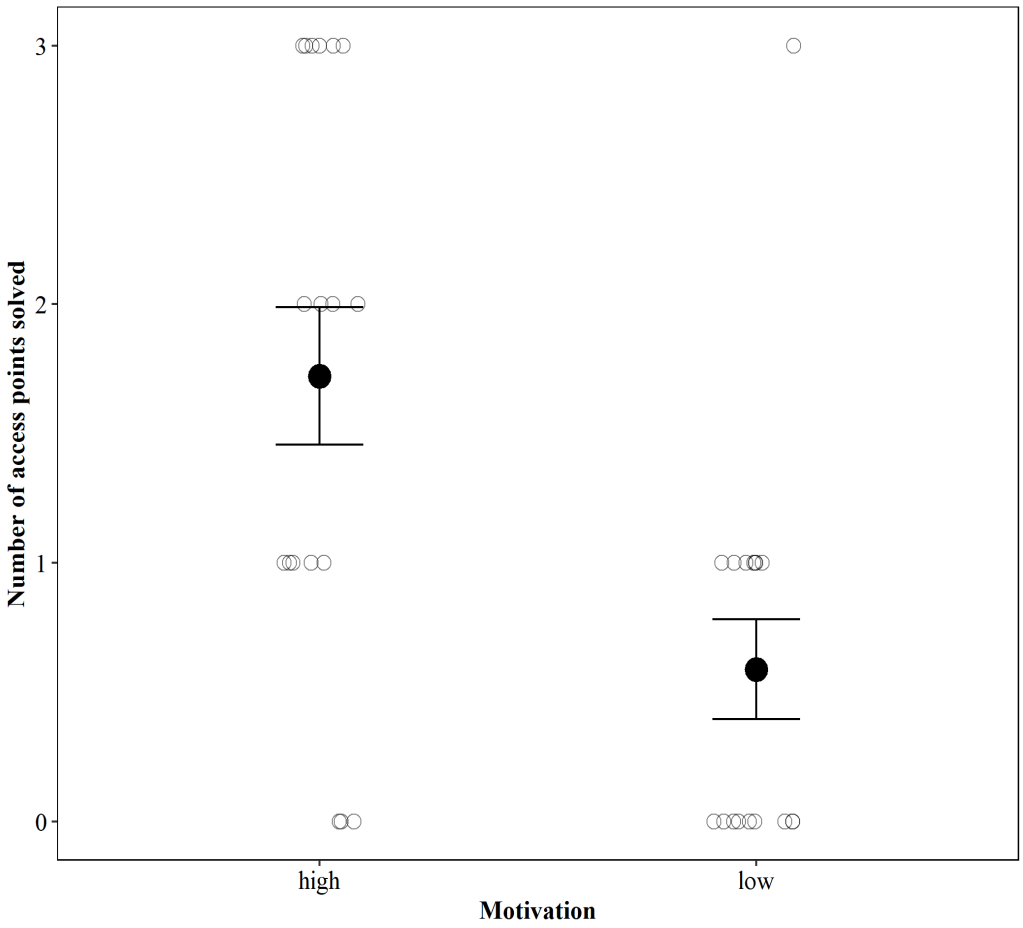

Figure 5. Effect of motivation (high or low) on the number of different access points solved (Table 4). Smaller points represent individual birds (which have been jittered along the X axis and rendered partially transparent to reduce overlap; as a result, any remaining overlap results in darker points). The large black points represent the mean number of access points solved in each motivation group; the T-bars represent SEs.

Repeatability

Latency to touch the device was repeatable but repeatability decreased when adjusted for significant fixed effects (Table 5). Accuracy was also repeatable but increased when adjusted for significant effects. Solving performance within a trial was also repeatable but repeatability disappeared entirely when adjusted for all significant fixed effects. To further investigate which factors were reducing the individual repeatability between the unadjusted and adjusted *R* values for solving access points within a trial, I removed each fixed effect individually and reran the repeatability model (see Table

5). Adjusted repeatability changed only when a significant fixed effect was excluded. Adjusted repeatability without accuracy was significant, and without motivation, while adjusted repeatability without previous experience only approached significance. There was no change in adjusted repeatability for any factor that did not affect solving performance.

Table 5 Repeatability (adjusted and unadjusted) estimates for the three main components of problem-solving behaviour during the experiment

Model	Repeatability	*R*	Confidence interval (lower, upper)	*P*
Latency to touch the device	Adjusted	**0.32**	**0.15, 0.45**	**<0.001**
	Unadjusted	**0.48**	**0.30, 0.61**	**<0.001**
Accuracy	Adjusted	**0.45**	**0.17, 0.52**	**<0.001**
	Unadjusted	**0.23**	**0.08, 0.38**	**0.001**
Solving access points within a trial	Adjusted	0.03	0, 0.17	0.40
	Unadjusted	**0.31**	**0.1, 0.46**	**<0.001**
	Adjusted: without accuracy	**0.18**	**0, 0.33**	**0.044**
	Adjusted: without motivation group	**0.21**	**0, 0.35**	**0.017**
	Adjusted: without previous experience	0.14	0, 0.29	0.076

Unadjusted values are from mixed models with only individual as a random effect. Adjusted values also include significant fixed effects for each of superscripts a, b and c as shown in Tables 1, 2 and 3, respectively. In addition, for superscript c adjusted repeatabilities are also shown when single fixed effects were removed. Significant results ($P < 0.05$) are highlighted in bold.

Discussion

Our study sought to explore factors that drive individual variation and repeatability at various stages of innovative problem-solving performance (Fig. 6). I showed that hunger-induced motivation affected multiple problem-solving stages, that previous experience influenced accuracy, and that hunger, accuracy and previous experience influenced problem-solving success. Personality and inhibitory control had little effect. Solvers of the opaque lever-pulling device tended to solve the lever on the multiaccess device. Furthermore, birds were more likely to solve the lever first, but showed no preference between the door and string. All traits were significantly repeatable; however, the repeatability of problem solving was explained entirely by motivation, accuracy and experience.

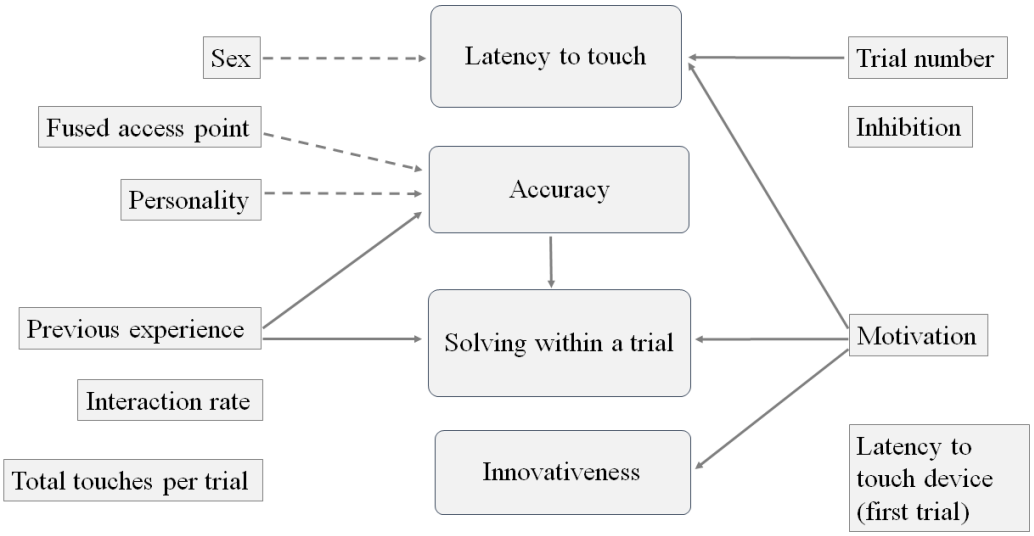

Figure 6. Schematic of the study's main results, with the four dependent variables aligned in the centre; arrows indicate influence of explanatory variables (left or right side). Dashed arrows indicate a nonsignificant tendency, no arrows refer to nonsignificant relationship. Note that no test was performed between previous experience and accuracy, and innovativeness because the two former variables are measured per trial, while the latter measure accrued across all trials.

Motivation Drives Innovation

Although motivation is often viewed as a confounding variable, if considered at all when examining mechanisms underlying problem-solving tasks (reviewed in Griffin

& Guez, 2014), it also underpins the 'necessity drives innovation' hypothesis (Reader and Laland, 2003). In support of this hypothesis, motivation was the major driver of an individual's latency to touch the device, to solve the same access point repeatedly and to innovate multiple times in my experimental set-up. Previous studies involving the Indian myna (*Acridotheres tristis*) reported that task engagement increased with increased food deprivation, thus facilitating problem solving (Sol et al., 2012; Griffin et al., 2014), but motivation itself did not predict problem solving (Griffin and Guez, 2014; van Horik and Madden, 2016). Likewise, the relationship between problem solving and motivation, as measured by body weight or body condition, is inconclusive: at times an effect is present (Laland and Reader, 1999a; Mateos-Gonzalez et al., 2011) and other times not (Cole et al., 2011; Thornton and Samson, 2012) but see Griffin & Guez, 2014, for full review). This variability in results across studies may be in part due to differences in how motivation is defined and how problem solving is measured. My results emphasize the importance of controlling for motivation and standardizing the length of time animals are food deprived in captive experiments, as well as acknowledging that not knowing an animal's motivational state may be a weakness of cognitive experiments conducted in the wild. Nevertheless, controlling for motivational effects generally is unlikely to be straightforward (Morand-Ferron and Quinn, 2011; Auersperg et al., 2012; Griffin and Guez, 2014; Morand-Ferron et al., 2016), not least because whether food deprivation removes, or just changes, individual variation remains unclear.

Personality

Considerable evidence suggests that personality traits defined by Réale et al. (2007) influence individual problem-solving performance (Greenberg, 2003; Sol et al., 2011; Johnson-Ulrich et al., 2018). However, in my study, personality selection lines with known genetic provenance for object neophobia and novel environment exploration did not predict latency to touch the device; nor did they predict problem-solving behaviour, in terms of success within trials, or the number of different innovations reached. I predicted that the effects of hunger-induced motivation could mask effects of artificially selected personality lines on problem-solving behaviour, but the interaction between motivation and personality had no effect on any problem-solving measure, suggesting that my ability to detect the effect of personality on an individual's capacity to solve problems was not confounded by motivation or vice

versa. Furthermore, while there was a nonsignificant tendency for slow birds to be more accurate, this did not translate into higher likelihood to solve problems or innovativeness for slow birds. Previous work in this same population, using a lever-pulling task, also found no link between personality and innovative problem-solving performance (Zandberg et al., 2017). The absence of an effect of personality on problem-solving performance in that study, and here, could be influenced by the composite nature of 'exploration' used in the selection lines (Verbeek et al., 1994). Moreover, latency to touch, which may be considered a measure of neophobia, may have been confounded with associative learning when considering latency to touch across multiple trials. Nevertheless, my results emphasize the challenge of examining links between personality traits and innovative problem solving, not least because of the inherently composite nature of both behaviours.

Inhibitory Control

Inhibitory control is an integral part of behavioural flexibility (Manrique et al., 2013; MacLean et al., 2014), both of which are beneficial for problem solving, allowing animals to overcome outdated information. Contrary to my predictions, individuals that exhibited high inhibitory control were no more likely to generate a novel solution to the task than those with low inhibitory control, even when the reward contingencies changed (i.e. when an access point was fused), a time when behavioural flexibility is required. This lack of correlation may be because changing one's behaviour is necessary but not sufficient to solve a problem (Logan, 2016a, 2016b). Moreover, the validity of the detour-reaching task as a test for inhibitory control remains under debate because performance does not necessarily correlate with other tasks that aim to measure inhibitory control, or because previous experience of transparency and persistence may influence performance (van Horik et al., 2018; Kabadayi et al., 2018). Neither Johnson-Ulrich (2018) nor Daniels et al. (2019) found a correlation between problem solving and inhibitory control in spotted hyenas (*Crocuta crocuta*) and raccoons (*Procyon lotor*) respectively, even when inhibitory control was measured using an alternative paradigm to the detour-reaching task. Thus I conclude that there is no case for motor inhibition affecting behavioural flexibility in the context of problem solving, but it remains possible that it reflects other facets of behavioural flexibility (reviewed in Bari & Robbins, 2013).

Previous Experience

Birds with previous experience of having solved the opaque lever device, or indeed any of the three access points during the main trials, were more accurate and had higher solving success in subsequent trials. Furthermore, performance improved with experience over repeated problem-solving attempts with regard to that particular solving method, perhaps owing to instrumental conditioning. Thus, attributing an individual's cognitive performance to how quickly it solves a problem, or its ability to solve multiple novel problems, may be a function of its previous experience (Rowe and Healy, 2014; Sih and Del Giudice, 2012). I acknowledge the constraints in controlling for all experiences that animals may have had with features of an experimental apparatus, especially if based on simple generalizable rules. Nevertheless, tasks could be designed such that they include multiple access points that vary in modality (e.g. smell and touch: sensory versus motor), in the appearance of the specific materials they use (e.g. white plastic versus black plastic) and/or in the required motor skills as I have attempted to do here (Overington et al., 2009; Auersperg et al., 2011; Manrique et al., 2013; Griffin and Guez, 2014). This paradigm may facilitate the testing of true innovations that are not confounded by previous experience, or alternatively, to explicitly test what kinds of experiences facilitate future innovations.

Repeatability, Pseudorepeatability and Positive Feedback

Our results demonstrate repeatable individual differences across two behaviours involved with problem-solving behaviour (latency to touch the device and accuracy when interacting with the device), and for problem-solving success itself. Adjusted and unadjusted repeatabilities differed for all three behaviours. For latency, repeatability decreased but remained significant after controlling for hunger-induced motivation, suggesting that some of the between-individual differences in the unadjusted repeatability were caused by hunger. In contrast, for accuracy, repeatability increased (and again remained significant) after controlling for the effects of previous experience, suggesting that some of the within-individual variation (the error component) in the unadjusted analysis was explained by previous experience. And for problem-solving success, repeatability was lost after controlling for accuracy, hunger and previous experience (i.e. consistent individual differences in problem-solving

performance were explained entirely by these three factors). Thus, repeatable problem-solving behaviour arose because of a complex set of interactions between different factors which themselves differed consistently between individuals.

The significance of these findings is tied to the nature of the specific factor involved. First, in the case of hunger, designed to manipulate motivation, each individual only experienced one of two treatments, a potentially reversible effect, suggesting that the component of the unadjusted between-individual difference explained by hunger was inflated, resulting in pseudorepeatability. Although some sources of motivation are probably permanent, either through a permanent environment (Wilson, 2018) or intrinsic motivation (Gajdon et al., 2014; Polizzi di Sorrentino et al., 2014; Taffoni et al., 2014; Ebel and Call, 2018), this pseudo measure demonstrates that failure to control for motivation caused by temporary factors can inflate the intrinsic between-individual differences that researchers are attempting to characterize; that is, those differences that are caused by a permanent environment or intrinsic effects. Second, accuracy explained some of the between-individual variation, suggesting that the mechanisms underlying accurate interaction with the device vary consistently between individuals themselves, and explain some of the between-individual differences in the problem-solving performance. It appears likely these mechanisms are intrinsic rather than reversible since motivation is controlled for in these analyses. Third, experience also caused some of the between-individual differences in problem-solving performance, and since experience is not reversible, and by definition carries forward into the next stage of the sequential problem-solving process, this suggests a positive feedback loop driving consistency between individual differences in problem-solving behaviour. Although the role of feedback loops in driving differences in individual behaviour is well known (Dall et al., 2004; Sih et al., 2015), and examples of positive feedbacks are common in nature (Kishida et al., 2011), to my knowledge none have explained consistent between-individual differences. In this case I assume the feedback caused by experience leads to a permanent effect, although it remains possible that individuals eventually forget the experience.

Our results highlight the challenges of characterizing consistent individual variation in sequential problem-solving performance as a measure of overall innovativeness. More generally, they provide a demonstration of how between-individual differences in innovation can be explained by inflated estimates of within-individual variation in

motivation, inflated between-individual variation in accuracy, and by feedback loops involving previous experience. Much of the focus in studies on the evolutionary ecology of behaviour in general has been on the evolutionary processes that drive intrinsic individual variation. My results support the idea that complex sources of variation underlying single traits are likely to make predicting the selective consequences of this variation challenging.

Acknowledgments

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Appendix

Table A1 Variable names and definitions

Variable	Definition
Latency to touch	Latency from start of trial to touching the device per trial
Personality	Second and third generation of bidirectionally selected personality lines for fast and slow exploring personality
Motivation	Two motivation treatment groups, low motivation (sated birds, fed 3 wax moth larvae 30 min before trial commences) or high motivation (birds that were food deprived 1 h before trial)
Trial number	Number of the trial
Fused trial	When any access point was fused in the trial
Bird identity	Identity code for each bird
Number of access points solved	Absolute number of different access points on the device solved by individual across all trials
Sex	Male or female
Inhibition score	Number of trials until individual reaches criterion in detour-reaching task (criterion = 4/5 consecutive successful trials)
Solving access points within a trial	Whether an individual has solved access points in a trial
Accuracy	Proportion of touches to functional access points on the device compared to all touches to the device per trial
Total number of touches per trial	Total number of touches to the device per trial

Previous experience	Whether in the current trial there was a functional, nonfused access point available to solve that they had solved previously; for the lever in the multiaccess task, this included whether they had experience solving the opaque device
Interaction rate	The number of total touches to any part of the device divided by duration of interacting with the device (time from first touch to last touch per trial)

Table A2 Minimum adequate model outputs from GLMM with factors affecting latency to touch the device per trial

Fixed effects	β ± SE	*t*	*P*
Intercept	4.25 ± 0.27	15.93	<0.001
Motivation group [a]	**1.19 ± 0.29**	**4.10**	**<0.001**
Trial number	**–0.09 ± 0.03**	**–3.30**	**0.001**
Sex [b]	–0.55 ± 0.30	–1.95	0.06

N = 226, df = 190, R^2 (marginal = 0.26, conditional = 0.47, AIC = 726.50). Random effect included bird identity (1.24; 95% confidence interval, CI = 1.08, 1.41) and the residual variance (0.51; 95% CI = 0.28, 0.95). Significant results ($P < 0.05$) are highlighted in bold.

[a] Low (reference level is high). [b] Male (reference level is female).

Table A3 Minimum adequate model outputs from GLMM with factors affecting accuracy per trial

Fixed effects	β ± SE	*t*	*P*

Intercept	0.27 ± 0.05	5.05	<0.001
Previous experience [a]	**0.36 ± 0.04**	**8.80**	**<0.001**
Personality [b]	0.12 ± 0.06	1.88	0.068
Fused trial	**–0.11 ± 0.04**	**–2.55**	**0.012**

N = 222, df= 187, R^2 (marginal = 0.34, conditional = 0.54, AIC = 49.42). Random effect included bird identity (0.24; 95% confidence interval, CI = 0.20, 0.27) and the residual variance (0.19; 95% CI = (0.13, 0.30). Significant results ($P < 0.05$) are highlighted in bold. [a] Yes (reference level is no). [b] Slow (reference level is fast).

Table A4 Minimum adequate model output from GLMM with factors affecting solving within trials

Fixed effects	β ± SE	z	P
Intercept	–2.42 ± 0.50	–4.88	<0.001
Accuracy	**3.91 ± 0.78**	**4.99**	**<0.001**
Previous experience [a]	**1.52 ± 0.42**	**3.65**	**<0.001**
Motivation group [b]	**–1.64 ± 0.48**	**–3.36**	**<0.001**

N = 224, df = 223, R^2 (marginal = 0.55, conditional = 0.58, AIC = 205.70). Random effect included bird identity (0.37; 95% confidence interval, CI = 0.33, 0.41) and the residual variance (0.13; 95% CI = 0.09, 0.25). Significant results ($P < 0.05$) are highlighted in bold. [a] Yes (reference level is no). [b] Low (reference level is high).

Table A5 Minimum adequate model outputs from GLM with factors affecting the number of different access points solved by an individual

Explanatory variables	β ± SE	z	P
Intercept	0.54 0.18	3.03	<0.005
Motivation group [a]	**–1.07 ± 0.36**	**–2.95**	**<0.005**

N = 35, df = 33, pseudo-R^2 = 0.23, AIC = 93.54. Significant result ($P < 0.05$) is highlighted in bold. [a] Low (reference level is high).

Table A6 Full model outputs from GLMM with factors affecting latency to touch

Fixed effects	β ± SE	*t*	*P*
Intercept	4.69 ± 0.90	5.22	<0.001
Motivation group [a]	**1.13 ± 0.44**	**2.58**	**<0.05**
Personality [b]	0.24 ± 0.46	0.51	0.62
Sex [c]	–0.49 ± 0.50	–0.97	0.35
Trial number	**–0.11 ± 0.51**	**–2.09**	**<0.05**
Previous experience [d]	–0.45 ± 0.28	–1.59	0.11
Inhibition score	–0.01 ± 0.07	–1.20	0.84

N = 128, *df*= 104. Data used in this model are from the subset of 22 individuals tested for inhibition score. Random effect included bird identity (1.24; 95% confidence interval, CI = 1.09, 1.42) and the residual variance (0.51; 95% CI = 0.28, 0.95). Significant results ($P < 0.05$) are highlighted in bold. [a] Low (reference level is high). [b] Slow (reference level is fast). [c] Male (reference level is female). [d] Yes (reference level is no)

Table A7 Full model outputs from GLMM with factors affecting accuracy per trial

Fixed effects	β ± SE	*t*	*P*
Intercept	0.21 ± 0.23	0.88	0.38
Interaction rate	0.00 ± 0.00	0.81	0.42
Previous experience	**0.34 ± 0.07**	**4.67**	**<0.00 1**
Personality [a]	0.16 ± 0.12	1.35	0.19
Motivation group [b]	–0.07 ± 0.11	–0.61	0.55
Fused trial	–0.19 ± 0.10	–1.89	0.06
Sex [c]	0.06 ± 0.13	0.49	0.62
Trial number	–0.00 ± 0.01	–0.29	0.76
Inhibition score	0.00 ± 0.02	0.31	0.75

N = 126, *df*= 99. Data used in this model are from the subset of 22 individuals tested for inhibition score. Random effect included bird identity (0.24; 95% confidence interval, CI = 0.15, 0.36) and the residual variance (0.19; 95% CI = 0.13, 0.30). Significant result ($P < 0.05$) is highlighted in bold. [a] Slow (reference level is fast). [b] Low (reference level high). [c] Male (reference level female).

Table A8 Full model outputs from GLMM with factors affecting solving access points within trials

Fixed effects	β ± SE	*z*	*P*
Intercept	–4.45 ± 1.49	–2.98	<0.001
Accuracy	**4.36 ± 1.07**	**4.05**	**<0.001**
Previous experience [a]	1.38 ± 0.80	1.72	0.08
Motivation group [b]	**–2.14 ± 0.69**	**–3.10**	**<0.01**
Personality [c]	–0.08 ± 0.64	0.13	0.90
Sex [d]	1.01 ± 0.73	1.38	0.17
Trial number	0.24 ± 0.16	1.44	0.15
Fused trial	–1.20 ± 1.22	–0.98	0.33
Total number of touches per trial	–0.00 ± 0.00	–1.37	0.17
Inhibition score	0.11 ± 0.10	1.11	0.28

N =126, *df* = 115. Data used in this model are from the subset of 22 individuals tested for inhibition score. Random effect included bird identity (<0.01; 95% confidence interval, CI = 0.0, 0.0) and the residual variance (<0.01; 95% CI = 0.0, 0.0). Significant results ($P < 0.05$) are highlighted in bold. [a] Yes (reference level is no). [b] Low (reference level is high). [c] Slow (reference level is fast). [d] Male (reference level is female).

Table A9 Full model outputs from GLM with factors affecting the number of different access points solved by an individual

Explanatory variables	β ± SE	*z*	*P*
Intercept	–0.67 ± 1.13	–0.59	0.55
Motivation group [a]	**–0.11 ± 0.53**	**–1.99**	**<0.05**
Personality [b]	0.23 ± 0.48	0.47	0.64
Sex [c]	–0.41 ± 0.54	0.76	0.45
Latency to touch the device	<0.001 ± <0.001	0.36	0.72
Inhibition score	<0.01 ± <0.01	0.66	0.51

N = 22, *df* = 16. Data used in this model are from the subset of 22 individuals tested for inhibition score. Significant result is highlighted in bold. [a] Low (reference level is high). [b] Slow (reference level is fast). [c] Male (reference level is female).

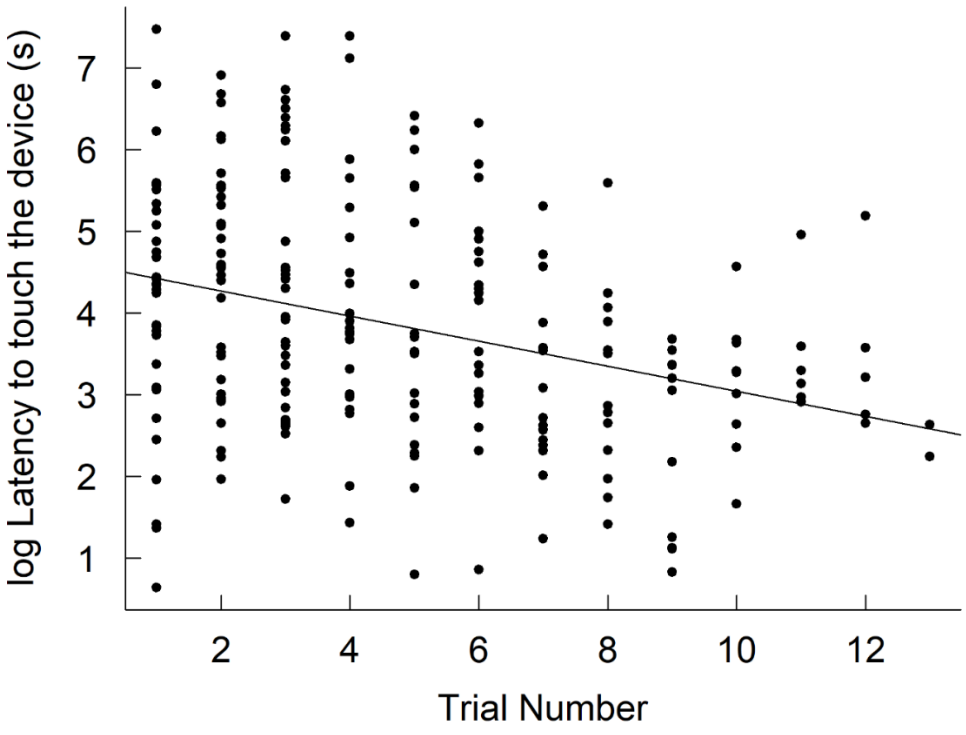

Figure A1. Latency to touch the device in relation to trial number. Data are log transformed in for scale purposes.

Chapter 3. Diet-induced changes to fatty acid composition are linked to personality, but not problem-solving performance, in wild Great tits (*Parus major*)

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Contributions: ACC GLD and JLQ designed the study. ACC and GLD collected the aviary-based data. ACC HLW and CI performed the fatty acid extractions. ACC conducted statistical analysis and led the manuscript writing. All authors contributed to interpretation of results and revisions of the manuscript.

Abstract

Food is fundamental for survival and reproduction, with food quality impacting not just physiology and body condition, but also cognition and behaviour. Diet-derived fatty acids are small organic compounds that support the energetic and physiological demands of animals, and are transported via the blood to the brain to regulate processes such as neurogenesis, neurite outgrowth and synaptogenesis. For example, arachidonic acid (an ω-6 polyunsaturated fatty acid) is crucial for normal development and functioning of the brain. In humans, deficiencies in fatty acids are linked to a broad range of psychiatric disorders, including depression, bipolar and attention deficit disorder. However past research has focused predominantly on humans and rodent model organisms, and the extent to which fatty acids influence behavioural variation in wild animals is largely unknown. The aim of this study was to explore how individual behavioural variation in captive wild great tits (*Parus major*) is influenced by diet and fatty acid profiles. First, I tested whether an all-seed diet or an all-insect diet differentially affected fatty acid composition in red blood cells, by comparing these compositions to the fatty acid compositions in red blood cells of their natural diet. Second, I investigated whether any changes in their exploration behaviour and problem-solving performance were associated with dietary manipulation and, or, changes in fatty acid profile. I found that the red blood cell fatty acid composition of

their wild diet differed after the seed diet but not the insect diet. Problem-solving performance was affected by diet, but not by fatty acid composition. In contrast, exploration behaviour was not affected by diet, but was negatively correlated with arachidonic acid specifically. Future research could investigate whether fluctuations in naturally occurring arachidonic acid across populations or between individuals correlate with exploratory behaviour.

Keywords: arachidonic acid, diet, exploration behaviour, fatty acid profile, great tits, *Parus major,* problem-solving performance.

Acronyms: arachidonic acid (AA), linoleic acid (LA), mono-unsaturated fatty acid (MUFA), oleic acid (OA), poly-unsaturated fatty acid (PUFA), saturated fatty acid (SFA).

Introduction

High quality food is fundamental for survival and reproduction (Lack, 1966), but not all food has equivalent nutritional value. Food quality is defined as the degree to which an animal's nutritional needs are fulfilled by the composition of accessible food (Müller-Navarra, 2008) and, provided their energetic needs are met, animals typically choose quality over quantity (Moore and Simm, 1985; Wheelwright, 1988; Whelan and Willson, 1994). For example, tree swallows fed on better quality food had a lower intake, faster growing rate, better body condition, lower metabolic rate and higher immune competence than their unsupplemented counterparts (Twining et al., 2016a). Furthermore, dietary composition (in particular dietary fatty acids) affects not only body condition, but also cognition (Greenwood and Winocur, 2005; Parrott and Greenwood, 2007; Mizunoya et al., 2013; Sandhu et al., 2017), via the development and maintenance of the brain and nervous system (Fernstrom, 2000; Wainwright, 2002). In school-age children, quality of food and cognitive performance are positively correlated (Glewwe et al., 2001) and abnormalities in dietary intake have a role in psychiatric disorders such as Attention Deficit Hyperactivity Disorder (ADHD) and depression (Rao et al., 2008; Liso Navarro et al., 2014). For generalist foraging species, dietary intake can vary greatly as a result of seasonal food variation or through processes such as competition or bottom up processes (e.g. the accessibility of resources across the food web) (Müller-Navarra, 2008; Twining et al., 2016b). The consequences of these processes may include limited food availability as well as

essential compounds such as certain fatty acids (Barón-Mendoza and González-Arenas, 2020). Thus, the cognition-diet relationship is especially important for species that engage in innovative foraging behaviour, and in species that differ in their willingness to explore novel environments, as these behaviours enable animals to effectively exploit food sources (Greenberg and Mettke-Hofmann, 2001; Ducatez et al., 2015b) and can also be affected by the nutritional components of the food they consume. Therefore, the aim of my study was to assess the link between diet, nutrition and behaviour in wild caught Great tits (*Parus major*).

Fatty acids are organic compounds that support the energetic and physiological demands of the animal (Glatz and van der Vusse, 1996; Kazantzis and Stahl, 2012), with links to fitness and survival (Müller-Navarra, 2008). For example, fledgling success and breeding success is predicted by the proportion of dietary omega-3 PUFA in tree swallows (*Tachycineta bicolor*) (Twining et al., 2018). Animals can synthesise fatty acids (in the cytosol of cells), by converting carbohydrates to pyruvate through the process of glycolysis (Stryer, 1995). However, "essential" fatty acids cannot be made in the body and therefore must be obtained through diet (Goodhart and Shils, 1980). Only two fatty acids are considered essential in animals; linoleic acid (LA) and α-linolenic acid (ALNA), a ω-6 and ω-3 PUFA, respectively. Free fatty acids are transported via the blood to the brain (Kaplan and Greenwood, 1998; Spector, 2001), to regulate processes such as neurogenesis, neurite outgrowth (developing neurons producing new outgrowths) and synaptogenesis (the formation of synapses between neurons) (Darios and Davletov, 2006; Wurtman, 2008; Cao et al., 2009). Fatty acids are broadly categorised into three groups, based on the saturation of hydrogen atoms and the number of double bonds, saturated fatty acids (SFA), mono-unsaturated fatty acids (MUFA) and poly-unsaturated fatty acids (PUFA). Variation in all three of these groups of fatty acids affects behaviour and cognition; in humans, for example, PUFA regulation is associated with clinical depression and Alzheimer's disease (Bazinet and Layé, 2014), and deficiency of PUFA during neural development can lead to schizophrenia and ADHD (as reviewed in Janssen and Kiliaan, 2014). Whereas MUFA have reversible effects on brain function, specifically memory (Dumas et al., 2016). In animals, spatial learning and memory is affected by differing levels of dietary fatty acids (as reviewed by Kaplan and Greenwood, 1998), and deficits of fatty acids are associated with spatial learning (Moriguchi et al., 2000; Moriguchi and

Salem, 2003), discrimination learning (Greiner et al., 2001) and working memory (Wainwright et al., 1998), as well as behavioural traits such as aggression (DeMar et al., 2006) and anxiety (Carrié et al., 2000). Notably, arachidonic acid (AA) is of particular importance for normal development and functioning of the brain (Wainwright, 2002), providing structure for neuronal cell membranes and together with docosahexaenoic acid, they influence signal transduction in the nervous system (Schuchardt et al., 2010) and modulate gene transcription (Raz and Gabis, 2009). AA can be derived from the diet, but can be synthesized by the essential LA, however the efficiency of such conversion is debated, and diet is likely to be more important for AA abundance in the body. Lower levels of AA have been implicated in a rise in psychiatric disorders such as bipolar disorder and depression (Wainwright, 2002; Rao et al., 2008; Lotrich et al., 2013), impulsivity (defined as defective control of decision making) in adults (Sanchez-Paez et al., 2020) and hyperactivity in children (Mitchell et al., 1987; Stevens et al., 1995; Hallahan and Garland, 2004). Despite the increasing numbers of studies reporting relationships between fatty acids and cognitive performance and behaviour (Barón-Mendoza and González-Arenas, 2020), research to date has focused predominantly on humans and rodent model organisms. The extent to which fatty acids influence behavioural variation in wild animals and the role of AA specifically is unknown.

Understanding the dynamics between diet and behaviour could help interpret the causes of individual variation in behaviour. Problem-solving behaviour and personality provide a framework for studying how animals adapt to and exploit novel resources (Reader and Laland, 2003; Sol et al., 2005; Ramsey et al., 2007; Cole and Quinn, 2012; Zandberg et al., 2017). Variation in problem-solving performance may, in part, be explained by animal personality as this can influence how individuals perceive and interact with their environment (Sih and Del Giudice, 2012). Alternatively, problem-solving performance and personality may be measuring separate behavioural traits (Cole et al., 2011), and therefore offer two distinct behavioural components that may be differentially affected by, for example, fatty acids. In light of the findings linking physiology and behaviour, examining diet dependent differences in the fatty acid composition may provide insight into variation in both problem-solving performance and personality.

Our aim in this study was to explore links between behaviour, diet and fatty acid composition in wild-caught great tits (*Parus major*). I manipulated their diet over a two-week period to test whether and how a seed diet or an insect diet differentially affected fatty acid composition (SFA, MUFA, PUFA, AA and linoleic acid (LA)). I predicted that if diet affects fatty acid composition in the blood, then I would find differences in fatty acid composition following dietary manipulation. Second, I investigated whether dietary manipulation or changes in the level of AA specifically (because of its link with brain development and function (Wainwright, 2002)), would lead to a change in their exploration behaviour and problem-solving performance relative to these behaviours prior to the dietary manipulation.

Methods

Study Site

I captured 36 great tits between January and March 2017 across four sites. Two sites were within Cork city (urban), 1.6 km apart, and two were in deciduous woodlands (rural) 23 km apart, and located at least 20 km from the urban sites. As part of the standard monitoring procedures, each bird was ringed with a unique metal British Trust for Ornithology (BTO) ring, and fitted on their opposite leg with a passive integrated transponder tag for individual identification. After ringing, the birds were transported to the aviary facilities at University College Cork, where they were housed individually in wire cages (45H × 50W × 60L cm) containing two wooden perches, a food bowl and a water bowl. All birds were visually but not acoustically isolated from one another and kept under a natural light regime. Birds were in captivity for 14 days and were released at their original capture site.

Dietary manipulation

From Day 2-13 of captivity, birds were given one of two different dietary treatments designed to reflect seasonal variation seen in the wild, reflecting changes in the availability of seed or animal food sources (Perrins, 1991; Vel'ký et al., 2011). The insect diet (n= 19) consisted of wax moth larvae (*Achroia grisella*) and mealworm larvae (*Tenebrio molitor*). Mealworms were provided *ad libitum*, and five wax worms were provided each morning and each evening (except during the problem-solving task). The seed diet (n = 17) consisted of sunflower hearts, peanuts and suet. Birds in the seed diet were provided with five mealworms and one wax worm on day seven of

captivity for welfare reasons. To limit more general nutritional deficiencies, all birds received vitamin powder mixed with their food and drops mixed in their water (AviMix®). Birds were assigned to treatment groups randomly, counterbalanced for age and sex.

Blood sampling

Blood samples were collected within 3 min after capture (Day 1) and again on Day 12. I collected 25µl of blood from the brachial vein with a heparinized syringe. Blood was immediately placed inside a microcentrifuge tube and into a container containing ice until they were brought back to the lab (within 2 hours). The plasma was separated from the blood cells by centrifuging at (10, 000 rpm for 10 min). All samples were stored at -20 degrees Celsius until biochemical analyses, when they were shipped to Lund University on dry ice, and then stored at -80 degrees Celsius.

Fatty acid extraction and gas chromatography/mass spectrometry (GC/MS) analysis

I extracted the total lipids from 5µl of red blood cells (RBCs). First, I added 50 µl chloroform:methanol (2:1 v/v) to the red blood cells and left it for 1 h at room temperature. I transformed the fatty acids into fatty acid methyl esters (FAMEs) through base methanolysis using 100 µl of 0.5 M KOH/Me (1 hr at 40°C). I terminated the reaction using 100 µl of 0.5 M HCl/Me, and extracted the FAMEs in 300 µl n-heptane (>99% pure, VWR Prolabo). I analysed samples using an Agilent 5975 mass spectrometer (MS) coupled to an Agilent 6890 gas chromatograph (GC), equipped with an HP-INNOWax PEG column (30 m, 0.25 mm i.d., 0.25 mm film thickness; Agilent). I used Helium as carrier gas at a constant flow of 1 ml/min. I programmed the GC oven temperature to 80°C for 1 min and then increased by 10°C/min to 230°C and held for 20 min. I analysed the chromatograms using Agilent ChemStation software. I identified FAMEs by comparison of retention times and mass spectra of known synthetic standards (Supelco 37 Component FAME mix, Sigma-Aldrich). I calculated the proportion of each individual fatty acid to the total fatty acid by dividing the peak area with the sum of all fatty acid peak areas in each sample. To reduce the risk of type I errors (false positives) due to multiple testing during the statistical analyses, I pooled individual fatty acids within a certain chemical class into three distinct groups; SFA, which predominantly serve the same function, to be used as metabolic fuel (Isaksson et al., 2017), MUFA and PUFA. The only individual fatty

acids I analysed were AA and LA, due to prior studies suggesting they are especially relevant for behaviour (Wainwright, 2002; Rao et al., 2008; Barón-Mendoza and González-Arenas, 2020). In preparation of statistical analysis, all fatty acid proportions were then logit-transformed ($\log(y/[1-y])$) (Warton and Hui, 2011).

Behavioural Assays

a) Exploration behaviour

Birds underwent an exploratory behaviour assay on Day 2 and on Day 13 of captivity. Each bird was released into a novel room (Verbeek et al., 1994) (measuring 3.5 × 3 × 2.5 m), with five artificial trees. The number of flights and hops between and within five artificial wooden trees, window ledges, support beams, door frames, and the entrances to the cages were recorded for two minutes by a hidden observer. Exploration scores were quantified by the sum of all the movements recorded during the trial. To encourage them to enter into the novel room the subject's cage was covered in black tarp, and the hole at the back of their cage that led into the room was opened; birds were then attracted through the hole into the bright room. If they did not willingly move from their home cage to the novel room within two minutes, they were encouraged through by an experimenter.

b) Problem-solving performance

To quantify individual foraging innovation, birds were presented with a problem-solving foraging task they had not previously encountered (Cooke et al., 2021). The multi access problem-solving apparatus (Figure A1) had three distinct solutions in order to obtain a preferred food reward (a wax moth larvae). The apparatus was an upright Perspex cylinder (height = 16cm, diameter = 5cm), with a platform holding the food reward. The platform was supported by a lever, which when pulled from the outside of the device caused the platform to drop, releasing the food reward below the device (solution 1). A second possible solution was to move a door that could be pushed left or right, to gain access to the food reward on the platform (solution 2). A third possible solution was to pull a string from the top of the device, which was attached to a second worm (solution 3). Each of these access points involved different motor action(s) including pulling (solution 1), pushing (solution 2) and coordinating both grasping and pulling (solution 3). To begin the problem-solving assay, a freely available wax worm was placed at the base of the problem-solving device to measure

birds' motivation to approach the apparatus and consume the wax worm. The birds were given the task in their home cage overnight from one hour before sunset to two hours after sunrise, once on Day 1 and once on Day 12 of captivity. Due to the length of the trial, birds were not food deprived for welfare reasons. During the first trial, all birds had the maintenance diet ad libitum. During the second trial, birds had access to their assigned diets ad libitum.

Data handling and statistical analysis

To explore the link between diet, nutrition and behaviour, I conducted three main analyses. First, I tested whether diet influenced fatty acid composition using four response variables: SFA, MUFA, LA and AA. I ran separate GLMMs using my four logit-transformed response dependent variables. Fixed effects included diet (three level factor: wild diet as measured on day 1 in captivity; insect diet; seed diet), age (adult or juvenile) and sex (male or female), while bird ID was nested within site as a random effect. Second, I examined whether diet (before and after manipulation) is associated with behaviour, by running two generalised linear mixed models (GLMMs), one with problem-solving performance as a response variable (binomial distribution) and a second with exploration behaviour as a response variable (Poisson distribution). Explanatory and random variables included were the same as in the first analysis. Finally, I investigated the effect of AA on behaviour, by running separate GLMMs for problem-solving performance and exploration behaviour as above. Fixed effects included AA, diet, age and sex, and sample (first or second), while bird ID was nested within site as a random effect. Data were analysed in R version 4.0.3 (R Core Team, 2020), using the *lme4* package (Bates et al., 2015). Model assumptions (collinearity, normality of residuals, homoscedasticity and overdispersion) were checked using the *performance* package (Lüdecke et al., 2020). I performed backwards stepwise selection, using both Akaike's information criterion (AIC) values, and likelihood-ratio tests to determine the model with the best fit (Thomas, 2015).

Data on problem-solving performance arising from this work has been published as part of another manuscript (Davidson et al., 2020).

Results

In total I identified 11 fatty acids (Table A1), from 59 samples (27 paired samples (before/after treatment) and 5 unpaired samples). One individual that did not partake in the behavioural assays was excluded from the analysis. The problem-solving task was solved 15 times, by 14 different individuals across both trial days, with one individual solving both before and after the dietary treatment. On Day 1, eleven (out of thirty-one) birds solved (3 lever, 8 door); on Day 12, four (out of thirteen) birds in the seed group solved (1 lever, 3 door) and none of the fifteen birds from the insect group solved the task. Exploration scores were obtained on Day 2 (min= 6, max= 46, median= 27.5) and on Day 13 (min= 9, max= 39, median= 27).

Diet treatment had an effect on SFA composition. There was a decrease in the proportion of SFA between the wild diet and the seed diet, ($\beta = -0.20 \pm 0.09$, $t= -2.16$, $p< 0.05$; Figure 1, Table 1). There was no difference in SFA proportion between the wild diet and the insect diet. There was a trend for males to have a higher SFA proportion than females ($\beta = 0.13 \pm 0.07$, $t = 1.80$, $p< 0.09$; Table 1).

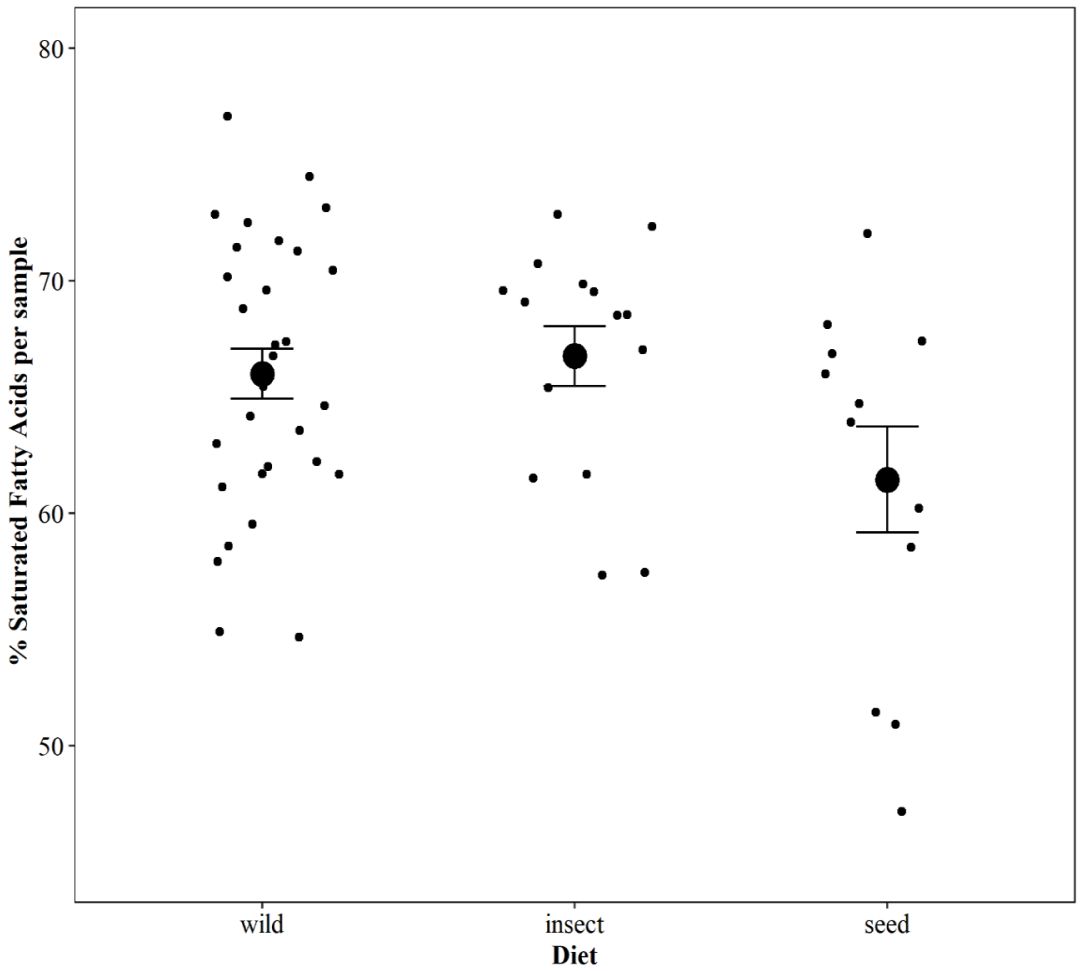

Figure 1 The effect of dietary treatment on the percentage of SFA per sample of wild great tits (n = 57; wild (n = 30), insect (n = 15), seed (n = 12), d.f. = 27). Points represent red blood cell sample (points have been jittered along the x-axis)**.** The large point represents the mean and the t-bars represent the standard error from the mean.

Table 1 Model outputs from GLMM testing dietary manipulation effects on the proportion of saturated fatty acids found in the cytoplasm of red blood cells (n = 57, d.f. = 27). Terms below the dashed line were not included in the minimum adequate model.

fixed effects	**estimate ± s.e.**	**t**	**p**
intercept	0.62 ± 0.06	10.77	0.00
insect diet[a]	0.03 ± 0.08	0.41	0.68
seed diet[a]	**-0.20 ± 0.09**	**-2.16**	**<0.05**
sex[b]	0.13 ± 0.07	1.80	<0.09
age[c]	-0.02 ± 0.08	-0.21	0.84

[a] insect or seed diet (reference level is wild diet), [b] male (reference is female), [c] juvenile (reference is adult).

Diet treatment had an effect on MUFA composition; there was an increase in the proportion of MUFA between the wild diet and the seed diet , ($\beta = 0.37 \pm 0.11$, $t = 3.29$, $p < 0.01$; Figure 2, Table 2). There was no difference in MUFA proportion between the wild and insect diet. There was no effect of diet on the proportion of AA (Table 3) or LA (Table 4).

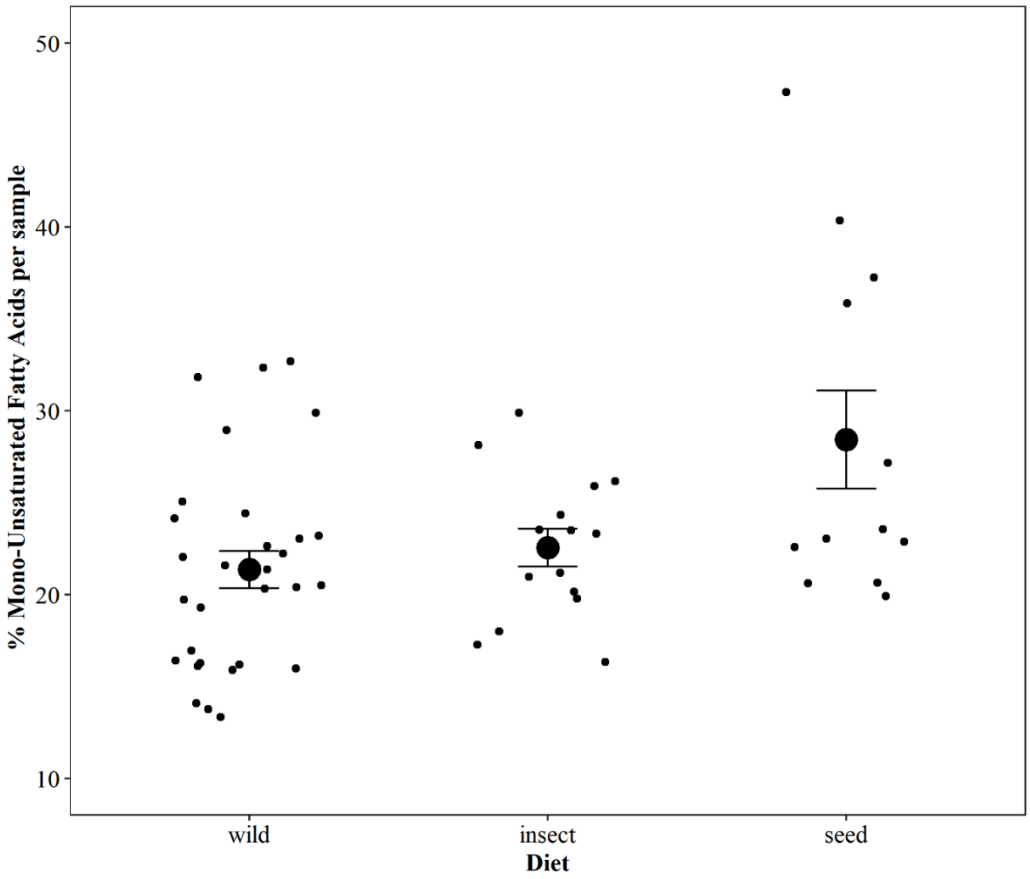

Figure 2 The effect of dietary treatment on the percentage of mono-unsaturated fatty acids (MUFA) per sample in wild great tits (n = 57; wild (n = 30), insect (n = 15), seed (n = 12), d.f. = 27). Points represent red blood cell sample (points have been jittered along the x-axis)**.** The large point represents the mean and the t-bars represent the standard error from the mean.

Table 2 Model outputs from GLMM testing dietary manipulation effects on the proportion of mono-unsaturated fatty acids found in the cytoplasm of red blood cells (n = 57, d.f. = 27). Terms below the dashed line were not included in the minimum adequate model.

fixed effects	**estimate ± s.e.**	**t**	**p**
intercept	-1.33 ± 0.06	-21.97	0.00
insect diet[a]	0.09 ± 0.11	0.82	0.42
seed diet[a]	**0.37 ± 0.11**	**3.29**	**<0.01**
age[b]	-0.03 ± 0.11	-0.30	0.76
sex[c]	-0.14 ± 0.10	-1.37	0.18

[a] insect or seed diet (reference level is wild diet), [b] juvenile (reference is adult), [c] male (reference is female).

Table 3 Model outputs from GLMM testing dietary effects on arachidonic acid found in the cytoplasm of red blood cells (n = 57, d.f. = 26). Full model is reported as it is not different from the null.

fixed effects	**estimate ± s.e.**	**t**	**p**
intercept	-6.01 ± 1.03	-5.86	0.00
insect diet[a]	-1.31 ± 0.98	-1.34	0.19
seed diet[a]	0.05 ± 1.06	0.05	0.96
age[b]	0.86 ± 0.94	0.91	0.37
sex[c]	0.124 ± 0.90	-0.14	0.89

[a] insect or seed diet (reference level is wild diet), [b] juvenile (reference is adult), [c] male (reference is female).

Table 4 Model outputs from GLMM testing dietary effects on the proportion of linoleic acid found in the cytoplasm of red blood cells (n = 57, d.f. = 26). Terms below the dashed line were not included in the minimum adequate model.

fixed effects	**estimate ± s.e.**	**z**	**p**
intercept	-2.20 ± 0.13	-17.26	0.00
insect diet[a]	-0.13 ± 0.08	-1.73	0.10
seed diet[a]	-0.15 ± 0.08	-1.76	0.09
age[b]	-0.07 ± 0.11	0.61	0.55
sex[c]	-0.02 ± 0.10	-0.20	0.85

[a] insect or seed diet (reference level is wild diet), [b] juvenile (reference is adult), [c] male (reference is female).

I found no effect of diet on exploration behaviour (see Table 5).

Table 5 Model outputs from GLMM testing dietary manipulation effects on exploration behaviour (n = 57, d.f. = 26). Full model is reported as it is not different from the null.

fixed effects	**estimate ± s.e.**	**t**	**p**
intercept	29.79 ± 2.92	10.20	0.00
insect diet[a]	0.39 ± 2.28	0.61	0.55
seed diet[a]	-1.34 ± 2.45	-0.40	0.59
age[b]	-4.28± 2.80	-1.53	0.14
sex[c]	-0.48 ± 2.69	-0.18	0.86

[a] insect or seed diet (reference level is wild diet), [b] juvenile (reference is adult), [c] male (reference is female).

I found an effect of dietary treatment on problem-solving performance. Birds were more likely to solve the task on their wild diet than on the insect diet (β = -0.37 ± 0.13, t = -2.74, $p < 0.05$; Figure 3, Table 6). Birds on the seed diet did not differ from the wild diet or the insect diet. I found no effect of age or sex on problem-solving performance.

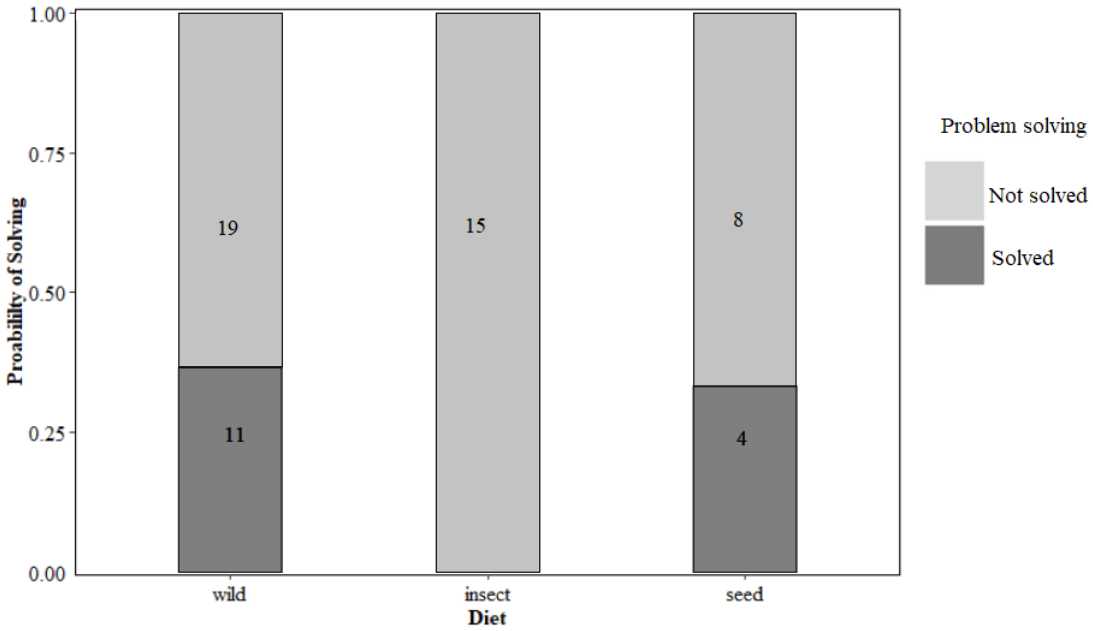

Figure 3 The proportion of great tits that solved the problem-solving task from the different diet treatments; wild (n = 30), insect (n = 15), seed (n = 12).

Table 6 Model outputs from GLMM testing dietary manipulation effects on problem-solving performance (n = 57, d.f. = 28). Terms below the dashed line were not included in the minimum adequate model.

fixed effects	**estimate ± s.e.**	**t**	**p**
intercept	0.37 ± 0.08	4.75	0.00
insect diet[a]	**-0.37 ± 0.13**	**-2.74**	**0.01**
seed diet[a]	-0.03 ± 0.14	-0.23	0.82
age[b]	0.17 ± 0.13	1.32	0.20
sex[c]	-0.04 ± 0.12	-0.35	0.73

[a] insect or seed diet (reference level is wild diet), [b] juvenile (reference is adult), [c] male (reference is female).

When controlling for the repeat sampling, there was a negative relationship between AA and exploration behaviour (β = -15.51 ± 4.36, t = -3.56, p< 0.05; Figure 4, Table 7). There was no effect of AA on problem-solving performance (see Table 8).

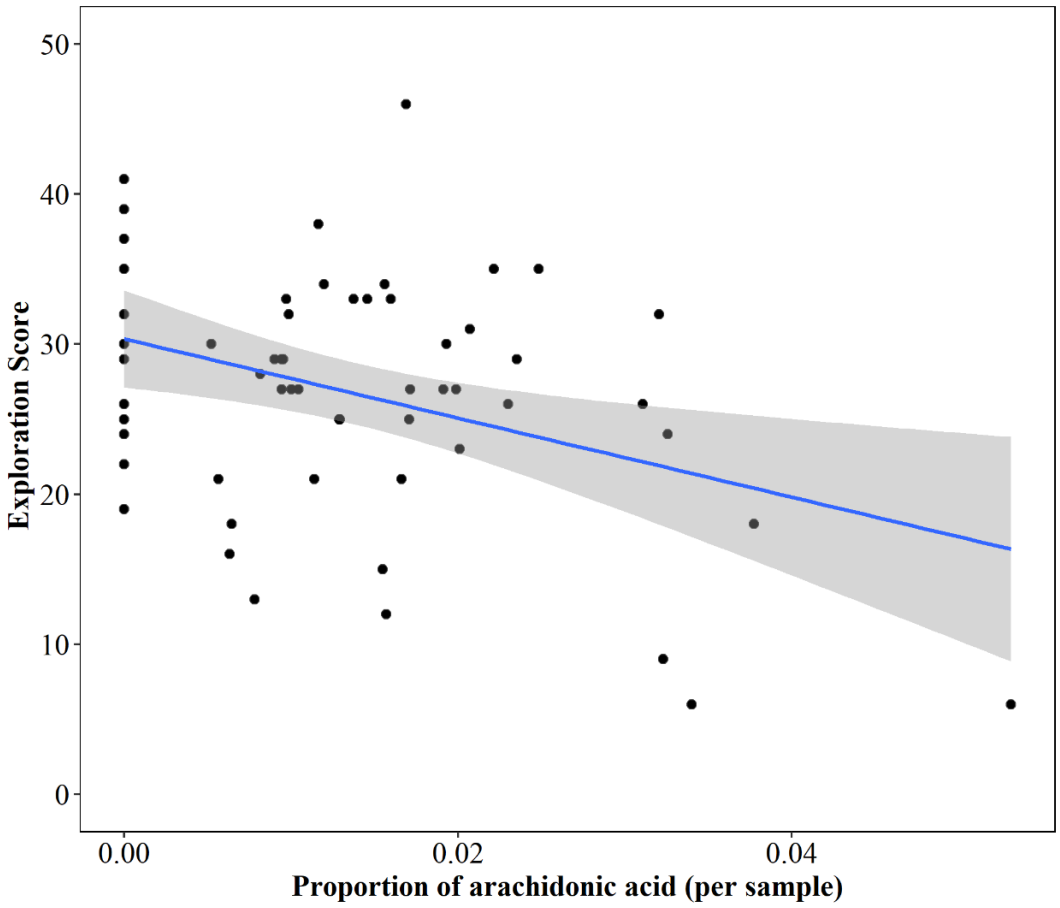

Figure 4 The effect of arachidonic acid on exploration behaviour in great tits. (n = 57; wild (n = 30), insect (n = 15), seed (n = 12), d.f. = 27). The blue line represents the line of best fit and the surrounding grey shade represents the standard error.

Table 7 Model outputs from GLMM testing the effects of arachidonic acid on exploration behaviour (n = 57, d.f. = 26). Terms below the dashed line were not included in the minimum adequate model.

fixed effects	**estimate ± s.e.**	**t**	**p**
intercept	3.44 ± 0.08	11.11	0.00
arachidonic acid	**-15.51 ± 4.36**	**-3.56**	**0.002**
age[a]	-3.58 ± 2.56	-1.40	0.17
sex[b]	-0.79 ± 2.46	-0.32	0.75
sample[c]	0.52 ± 1.85	-0.28	0.78

[a] juvenile (reference level is adult), [b] male (reference level is female), [c] second (reference level is first).

Table 8 Model outputs from GLMM testing the effects of arachidonic acid on problem-solving performance (n = 57, d.f. = 27). Full model is reported as it is not different from the null.

fixed effects	**estimate ± s.e.**	**z**	**p**
intercept	-2.10 ± 0.96	-2.19	0.03
arachidonic acid	-16.44 ± 28.91	-0.57	0.57
age[a]	0.89 ± 0.79	1.12	0.26
sex[b]	-0.33 ± 0.70	-0.47	0.63
sample[c]	-1.31 ± 0.69	-1.92	0.06

[a] juvenile (reference level is adult), [b] male (reference level is female), [c] second (reference level is first).

Problem-solving performance was not influenced by motivational differences to consume the food reward, as all birds were equally likely to consume the motivational worm that was made freely available to them, regardless of dietary treatment (insect β = -0.60 ± 2.69, z= -0.02, p = 0.98; seed β = 0.00 ± 0.00, z= 0.00, p = 1.00, Table 9).

Table 9 Model outputs from GLMM testing the effects of dietary treatment on acquisition of motivational worm during problem-solving performance (n = 57, d.f. = 27). Full model is reported as it is not different from the null.

fixed effects	**estimate ± s.e.**	**z**	**p**
intercept	5.00 ± 6.33	0.00	1.00
insect diet[a]	-0.60 ± 2.69	-0.02	0.98
seed diet[a]	0.00 ± 0.00	0.00	1.00
age[b]	2.40 ± 0.00	0.00	1.00
sex[c]	-3.69 ± 6.33	0.00	1.00

[a] insect or seed diet (reference level is wild diet), [b] juvenile (reference is adult), [c] male (reference is female).

Discussion

I found that the seed diet, but not the insect diet altered fatty acid composition in red blood cells. In birds that were assigned the seed diet, there was a decrease in SFA proportion, an increase in MUFA, when compared to the wild diet fatty acid profiles of the birds. Neither LA nor AA changed relative to the wild diet. I found no difference in fatty acid composition between the insect diet and wild type diet. While I found a change in problem-solving performance, this was not associated with any of the fatty acid profiles. By contrast, exploration behaviour did not change due to diet, yet slow explorers had a higher proportion of arachidonic acid.

Sunflower seeds and peanuts are common bird feeder foods that are provided during the winter. Both peanuts and sunflower seeds are associated with high levels of MUFAs and PUFAs, specifically, OA and LA (Andersen et al., 1998; Akkaya, 2018), yet contain little to no AA (Andersen et al., 1998; Aguillón-Páez et al., 2020). My study showed an increase in MUFAs among birds in the seed diet treatment, in comparison to levels present in their wild diet. This suggests that the birds consumed more seeds and peanuts in the aviary than in the wild, indicating that birds in the wild must have been eating substantial amounts of natural food items, and did not rely on supplementary seeds and peanuts freely available at feeders. Additionally, MUFA can be synthesized from SFA; birds may be metabolising fatty acids differently in order to meet the more demanding needs of the wild, compared to the aviary. In contrast, I

saw no change in fatty acid composition when birds were given an all insect diet compared to their wild diet. The similarity between the wild and insect diet suggests that the birds were predominantly consuming animal prey in the wild, since ingested food strongly correlates with plasma fatty acid profiles (Hulbert and Abbott, 2012). However, the wild winter diet of great tits is primarily plant based and the summer diet is predominantly insect based (Perrins, 1991; Vel'ký et al., 2011) and these seasonal differences in dietary preference correlate with the plasma fatty acid profiles (Andersson et al., 2015). Therefore, the unexpected similarities may be a result of selective mobilisation, where fatty acids may have been selectively mobilised from adipose tissue (Raclot, 2003; Price et al., 2008, 2013), in order to meet the physiological demands of the winter season, such as thermoregulation, to combat the lack of insects in their diet, or possible physiological effects of captivity. Future work should focus on investigating seasonal variation, examining whether we can draw similarities between the dietary treatments and the summer diet fatty acid profiles or the summer and winter wild fatty acid profiles.

Birds on the insect diet treatment were less likely to solve than when on the wild diet or the birds on the seed diet. However, I show that this difference in problem-solving performance does not stem from differences in proportion of arachidonic acid, suggesting that changes to problem-solving performance arose due to some other mechanism. Captivity is known to affect motivation (McCune et al., 2019), and differences in motivation may dictate whether animals participate (van Horik & Madden), and solve tasks (Griffin and Guez, 2014; Cooke et al., 2021). In the current study, only the birds in the insect group showed a decrease in problem-solving performance, suggesting that it is not captivity itself driving the difference in problem-solving performance. While I cannot exclude the possibility that birds on the insect diet were less motivated to work for the reward in the apparatus, all birds consumed the wax worm that was freely available outside of the apparatus, indicating that they were motivated to eat the same highly preferred food reward that was inside the device. Results arising from this same experiment show that the insect diet caused parallel changes to the gut microbiome and problem-solving performance (Davidson et al., 2020), where a decrease in diversity of the microbiome was correlated with problem-solving performance, which suggests that the microbiome, rather than diet, may be mediating such behavioural plasticity.

Exploration behaviour was correlated with arachidonic acid, yet neither exploration behaviour nor AA were affected by diet. The lack of effect of dietary manipulation on exploration behaviour, is perhaps due to exploration behaviour being a personality measure which remains consistent over time and different contexts (Réale et al., 2007). Although personality does not preclude plasticity in behaviour (Dingemanse et al., 2010), because by definition, rank order differences may be maintained even when a personality trait is flexible, I found no evidence of that either captivity or diet caused a change in personality. Nevertheless, individuals that were more exploratory had less AA in their red blood cells. Previous studies have found similar results in captive animals. In pigs (*Sus scrofa domesticus*) a decrease in the precursors of AA led to an increase in exploratory behaviour (Clouard et al., 2015), and in lemur mice *(Microcebus murinus*), a decrease in exploratory behaviour was observed alongside an increase in n-3 fatty acids (Languille et al., 2012). Whether AA and exploratory behaviour are intrinsically linked, or whether co-variation of these two variables are explained by another mechanism not tested here, requires further investigation. Specifically, because there was no change in AA from the diet in my study, future work would benefit from manipulating AA to investigate any effects on behaviour. Such an approach in humans has shown that supplementation of essential fatty acids has alleviated the symptoms of ADHD in children (Raz and Gabis, 2009). Future research could also measure fluctuations in naturally occurring AA across urbanised gradients and whether these changes correlate with exploratory behaviour. Given the extensive influence fatty acids have on brain development, physiology, cognition and behaviour (Wainwright, 2000), the variation and effects of fatty acid profiles in wild animals requires more in-depth investigation.

Conclusions

Dietary changes lead to differential changes in fatty acid composition in the red blood cells of great tits. Diet was linked to changes in problem-solving performance in great tits, but this was not due to changes in fatty acid profile since there was no association between problem-solving performance and AA. AA was negatively correlated with exploration behaviour, but diet did not affect either of these variables. Future work should focus on three lines on examination: (i) seasonal variation, to examine similarities between the dietary treatments and summer diet fatty acid profiles, (ii) differences in fatty acid profiles between adults and juveniles, how this might

influence exploration behaviour and cognition and (iii) targeted manipulations of fatty acids shown to correlate with variation in behaviour.

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APPEDIX

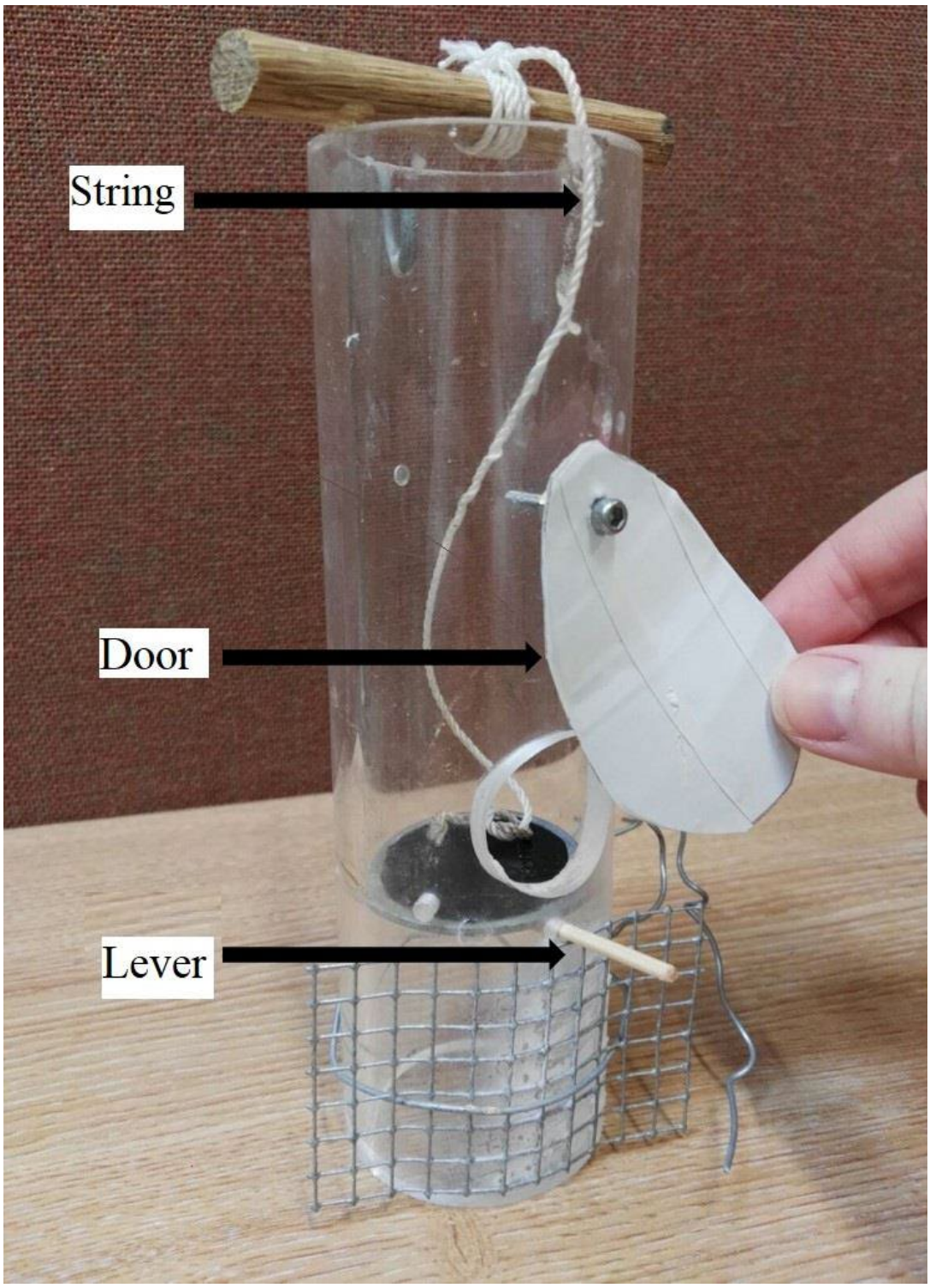

Figure A1 The multi-access problem-solving device given to birds in their home cage. The apparatus has three different access types to retrieve the food reward inside; a lever, a swing door, and a string.

Table A1. Summary table of all fatty acids present in the red blood cells of wild great tits.

Common name	C:D	Fatty acid group
Palmitic acid	16:0	SFA
Margaric acid	17:0	SFA
Stearic acid	18:0	SFA
Arachidonic acid	20:0	SFA
Behenic acid	22:0	SFA
Lignoceric acid	24:0	SFA
Lignoceric acid	24:0	SFA
Oleic acid	18:1n-9	MUFA
cis-Vaccenic acid	18:1n-7	MUFA
Paullinic acid	20:1n-9	MUFA
Linoleic acid	18:2n-6	PUFA
Arachidonic acid	20:4n-6	PUFA

C:D = number of carbon: double bonds, SFA = saturated fatty acid, PUFA = ω -6 polyunsaturated fatty acid, and MUFA = monounsaturated fatty acid.

Chapter 4. Non-lethal effects of predators on prey in the context of spatial learning and behavioural flexibility

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Contributions: ACC GLD and JLQ designed the study. ACC and IDLH collected the data. ACC conducted statistical analysis and led the manuscript writing. All authors contributed to interpretation of results and revisions of the manuscript.

Abstract

The ability to forage in a complex, fluctuating environment is essential for survival and reproduction. Animals need to successfully search, locate and return to a food source, while being proficient at switching between these behaviours when appropriate, and simultaneously remain vigilant for predators. Spatial learning facilitates these foraging processes, but little is known about the effect of predation risk on spatial learning and cognition. I hypothesised that varying levels of predation risk would influence learning speed, behavioural flexibility and memory in a foraging task. To test this, I exposed wild caught great tits (*Parus major*) to an array of four feeders, where they had to learn to locate their specific rewarding feeder during two separate phases (initial and reversal learning), under the presence of three escalating levels of predation risk (low, medium and high). Contrary to my expectations, predation risk had no effect on initial learning speed. However, birds under highest predation risk demonstrated greater behavioural flexibility (as measured by reversal learning speed) compared to those under low predation risk. Finally, individuals under the highest degree of predation risk displayed worse memory for their reward location than those under medium or low predation risk. My study demonstrates that overall varying levels of predation pressure do not affect spatial learning. However, in the high predation risk group, I found individuals who were fast reverse learners were slow initial learners and had poorer memory. Future work should focus on disentangling the association between initial and reversal learning under high predation risk and whether reduced memory retention in individuals under high pressure arises from causation or correlation.

Key words: Spatial learning, predation, cognition, behavioural flexibility, memory retention, wild Great tit.

Introduction

Cognition, the process through which animals take in and utilise information (Dukas, 2004; Shettleworth, 2009), is central to most behaviour (Cate and Healy, 2017). Understanding the role of cognition is fundamental to ecology and evolution because cognitive performance (the realised outcome of cognitive ability) varies between species and individuals, and is associated with social structure (Langley et al., 2020a), sexual selection (Boogert et al., 2008), reproduction (Grieco et al., 2002; Cauchard et al., 2013) and survival (Pravosudov and Roth II, 2013; Whiteside et al., 2016; Madden et al., 2018). Some variation in cognitive performance is caused by permanent effects (e.g., genetic or maternal effects, (Lofdahl et al., 1992; Mery and Kawecki, 2002; Langley et al., 2020b)), but many ecological factors induce more temporary variation in cognitive performance (e.g. motivation, (Cooke et al., 2021); social rank, (Thornton and Samson, 2012) and seasonal effects (Quinn. et al., 2016)). Thus cognitive performance is frequently context dependent and highly plastic (Dukas, 2004). Nevertheless, we still have a limited understanding of the role of ecological context in shaping variation in cognitive performance in wild animals. Therefore, the aim of this study is to examine the degree to which ecological drivers, such as predation risk, affect the performance of key cognitive behaviours involved in foraging, specifically spatial learning, behavioural flexibility and memory retention.

Foraging animals must search, identify and return to feeding patches (Healy and Hurly, 2004), using a process of detecting and filtering information that involves a wide range of cognitive mechanisms (Kamil and Bond, 2006), such as learning (Kamil and Yoerg, 1982; McNamara and Houston, 1985), behavioural flexibility (Dyer et al., 2014) and memory (Healy and Hurly, 2017). Spatial learning is particularly important in foraging (Pravosudov and Clayton, 2002), as the ability to remember specific locations enables animals to adapt to a diverse range of challenges, including surviving in harsh climates (Sonnenberg et al., 2019), and avoiding areas with high predation risk (Magurran et al., 1995). Secondly, behavioural flexibility enables individuals to adapt their behaviour to changes within their environment (Brown and Tait, 2014), and is particularly beneficial for foraging animals when food sources vary over time,

e.g. seasonally (Sonnenberg et al., 2019), as a result of competition or through natural depletion of resources (Gibeault and MacDonald, 2000). Lastly, memory (the ability to retain information) is often crucial to foraging (Burns and Rodd, 2008), as animals need to revisit profitable foraging locations and avoid depleted ones (Bateson et al., 2003). Learning, behavioural flexibility and memory can occur simultaneously (Brydges et al., 2008) and therefore are likely to interact with one another to determine foraging success. For example, behaviourally flexible individuals can learn more readily under changing contingencies, however higher behavioural flexibility is linked to reduced memory retention (Tello-Ramos et al., 2019). Moreover, environmental conditions are also known to affect these cognitive processes (Morand-Ferron et al., 2011; Quinn et al., 2016; Sonnenberg et al., 2019; Tello-Ramos et al., 2019; Reichert et al., 2020). However, the extent to which these traits are affected by varying levels of predation or whether there are carry over effects remains unknown. To better understand the effects of predation risk on these cognitive mechanisms involved in foraging, I measured spatial learning ability, behavioural flexibility and memory under simulated predation threat.

Predation is one of the fundamental drivers of evolution (Yoshida et al., 2003), affecting population dynamics (Hik, 1995; Turchin, 2003) and driving changes in morphology and animal behaviour (Lima and Dill, 1990; Cresswell et al., 2003). Animals are often at high-risk of predation while foraging (Lima and Dill, 1990; Brown, 1999), due to increased exposure (Verdolin, 2006) and a limited field of view (Whittingham et al., 2004), therefore they must respond to predation risk appropriately in order to survive. Animals are alerted to predation risk through cues (Lima and Dill, 1990). Direct predation cues come from the predator (Lima, 1998) and can include urine or sound (Thorson et al., 1998), as well as the physical presence of the predator. Conversely, indirect predation cues consist of second-hand information, such as alarm calls from disturbed conspecifics (Lind et al., 2005) or dead conspecifics (Hedrick and Kortet, 2004). Previous work has focused on how these predation cues effect foraging decisions such as the trade-off between foraging and vigilance (Cresswell et al., 2003; Whittingham et al., 2004). However, the effects of predation risk on the cognitive processes involved foraging are still poorly understood.

The aim in this study was to determine the effect of a key ecological variable, predation risk, on spatial learning performance, behavioural flexibility and memory,

in the context of foraging in wild great tits (*Parus major*). I exposed wild caught great tits to an array of four feeders, where they had to locate and repeatedly visit their specific rewarding feeder during two separate phases (initial and reversal learning), under one of three predation treatments (high, medium or low). Following a three-day break, great tits were exposed to the feeding array once more, for a memory retention assay in the absence of the predation treatment. I have two different hypotheses. First, I hypothesised that learning and reversal learning speed would differ between birds experiencing different predation cues. I predicted that if predator vigilance detracts from foraging, because more time is spent on the lookout for predators, then birds under the high-risk of predation pressure should take the longest to learn. Furthermore, I suspected there would be an association between reversal learning speed and memory. I predict that if individuals had a poor reversal learning speed because of the influence of predation risk, then they would also have poor memory retention.

Methods

Housing and study site

Using mist nests and potter traps, I caught 36 wild great tits (*Parus major*) from four different field sites of mixed deciduous woodland, separated by at least 2km from one another. They were transported in cloth bags to a purpose-built aviary at University College Cork, where they were held for 8 to 16 days, to partake in behavioural experiments. Birds were housed individually and visually isolated from each other, with a nine-hour light cycle (8am to 5pm), during which time I played a deciduous woodland birdcall mix of blackbird (*Turdus merula*), long-tailed tit (*Aegithalos caudatus*), goldcrest (*Regulus regulus*) and treecreeper (*Certhia familiaris*), at a low volume to mimic a more natural environment. Cages were 62cm x 60cm x 50cm with solid walls, ceiling and roof, with two perches. Birds had *ad libitum* access to sunflower seeds, peanuts and water, as well as mealworms twice daily, and one wax worm in the evening. Each individual was given a unique metal British Trust for Ornithology (BTO) ring, and a passive integrated transponder tag for individual identification and detection during the learning experiment.

Predator treatment

For the duration of the experiment each bird was randomly assigned to one of three different predator treatment groups; flying aerial predator, hereafter referred to as high-risk (a stuffed sparrow hawk or a plastic hawk), an alarm call from a conspecific, hereafter referred to as medium risk (Bluetooth speaker in room) or a blackbird song, hereafter referred to as low risk and was treated as a control condition (Bluetooth speaker in room). Playback tracks were curated from live recordings of Great tits (*Parus major*) at their nestbox during the breeding season, while the blackbird control calls were downloaded from Xeno-canto (for full list of tracks, please see Appendix 1 in supplementary). Birds under a playback treatment were randomly assigned one of six different playback tracks, to ensure that there was no effect of the specific track used (Gentry et al., 2020). All tracks were created at a set amplitude of 70 dB SPL recorded from one metre. The predator treatment lasted ten seconds and was delivered twice within each hour-long trial, once at the beginning and once at 30 min.

Spatial learning

Four automated feeders were arranged in a square, spaced 1 m apart in the centre of the test room, with the radio frequency identification (RFID) perch facing outwards away from the other feeders. RFID antennae detected individuals' PIT tags every time they landed, providing visit location and visit timing information. In an attempt to limit visits to feeders that were not goal-directed towards obtaining food - i.e. to limit the extent to which birds landed on the feeders simply because they needed somewhere to sit rather than to make a choice - I placed four wooden trees throughout in the room and one small fake fir tree to provide alternative perches to the feeders. All birds were food deprived for one hour before each trial and were tested individually in the test arena. For the learning experiment (including habituation, training, initial and reversal learning), trials lasted one hour per day continuing for up to one week or until they met each phase criterion (described below).

To habituate the birds to the room and the foraging array, I used four transparent feeders containing visible sunflower seeds, in the same array as described above. I considered birds to be habituated when they consumed a minimum of ten sunflower seeds from any of the four feeders during one trial. During the training phase, birds had to feed on the same feeders in the array as described above, but with the feeders entirely opaque so there was no visible food reward. All feeders contained seeds and

birds completed training when they made ten visits to any of the feeders in one trial session.

For the initial learning experiment, birds were randomly assigned a single rewarding feeder (i.e. contained seeds), with the restriction that they were not assigned to the feeder they preferred (visit majority) during the training trials (if there was one). I define learning as 80% correct visits over ten consecutive visits (Reichert et al., 2020). I define learning speed as at the number of visits made until the individual first met the learning criterion. PIT-tag detections at the same feeder within a two second duration were considered as one visit (Evans et al., 2018). If a bird reached learning criterion, it was advanced to the reversal learning phase the following day. Here, the rewarded location was changed to a different randomly selected feeder and they had to reverse learn (same criterion) the new rewarded location. Birds were allowed seven days to reach the criterion for each learning phase.

Memory

If birds reached criterion during the reversal learning, birds were presented with a memory test after a three-day retention interval. Using the same feeder array as in the reversal phase, I recorded their memory score as the number of errors before landing on the feeder that was assigned to them during the reversal learning task. In this phase there was no predator treatment (i.e. alarm call or sparrowhawk) and none of the feeders were rewarded. I chose to omit predator treatment as I aimed to measure their memory relative to the reversal phase treatment only. Feeders were empty of seeds so that their choices were not affected by the presence of rewards

Statistical analysis

To test whether learning speed, for initial learning as well as reversal learning, was influenced by predator treatment, I conducted two negative binomial general linear models with log-link function in R version 3.6.1. I used this model to account for over-dispersion because the dispersion statistic theta (h) was greater than 15 (Thomas, 2015). The response variable was the number of visits to criterion (either initial learning or reversal learning) and fixed factors included in this model were predator treatment (high, medium or low, with low as the reference category), sex and age (adult or juvenile, where juvenile is hatched in the previous year and adult is hatched at least two years ago).

After the initial data exploration, I conducted a *post hoc* analysis, to investigate the difference in learning speeds between reverse and initial learning, and the effect of the predator treatment. I ran a negative binomial generalised linear mixed model, fit with a log-link function, using the R package glmmADMB (Fournier et al., 2012; Skaug et al., 2018), as the initial generalised linear mixed model revealed an overdispersion statistic value of 18 (Thomas, 2015). The response variable was visits to criterion and fixed factors included were experiment phase (initial or reverse) predator treatment, sex and age. I included the interaction between experiment phase and predator treatment, to account for any potential influence of predator treatment on learning. Individual ID was included as a random effect to account for repeated measures for each learning phase.

Finally, to test the effect of spatial learning speed and predator treatment on memory, I conducted a negative binomial generalised linear model fit to account for over dispersion (as in the initial generalised linear model revealed an overdispersion statistic value of 2.3 (Thomas, 2015). The response variable was the memory score (errors before landing on their reverse feeder), and fixed effects were reversal learning speed, predator treatment, sex and age. I also tested for an interaction between reversal learning speed and predator treatment to account for individual reversal learning being measured under one specific predator treatment.

For all analyses above, models were compared using Akaike's information criterion (AIC) values, and likelihood-ratio tests to determine the model with the best fit. After model selection, any interaction or explanatory variable was considered significant if it had a p-value higher than the threshold (0.05).

Results

Thirty-six birds (19 female and 17 male; 19 junveniles and 17 adults)were taken into the aviary, seven birds dropped out before the initial learning phase as they never habituated to the experimental set up. Four birds (low risk = 2 and high-risk = 2) never learned the location of their initial rewarded feeder and therefore did not progress to the reversal learning phase. Twenty-five birds completed the reversal learning and subsequent memory stage (12 female and 13 male; 12 juveniles and 13 adults).

I found no effect of predator treatment on initial learning speed (see Figure 1 and Table 1).

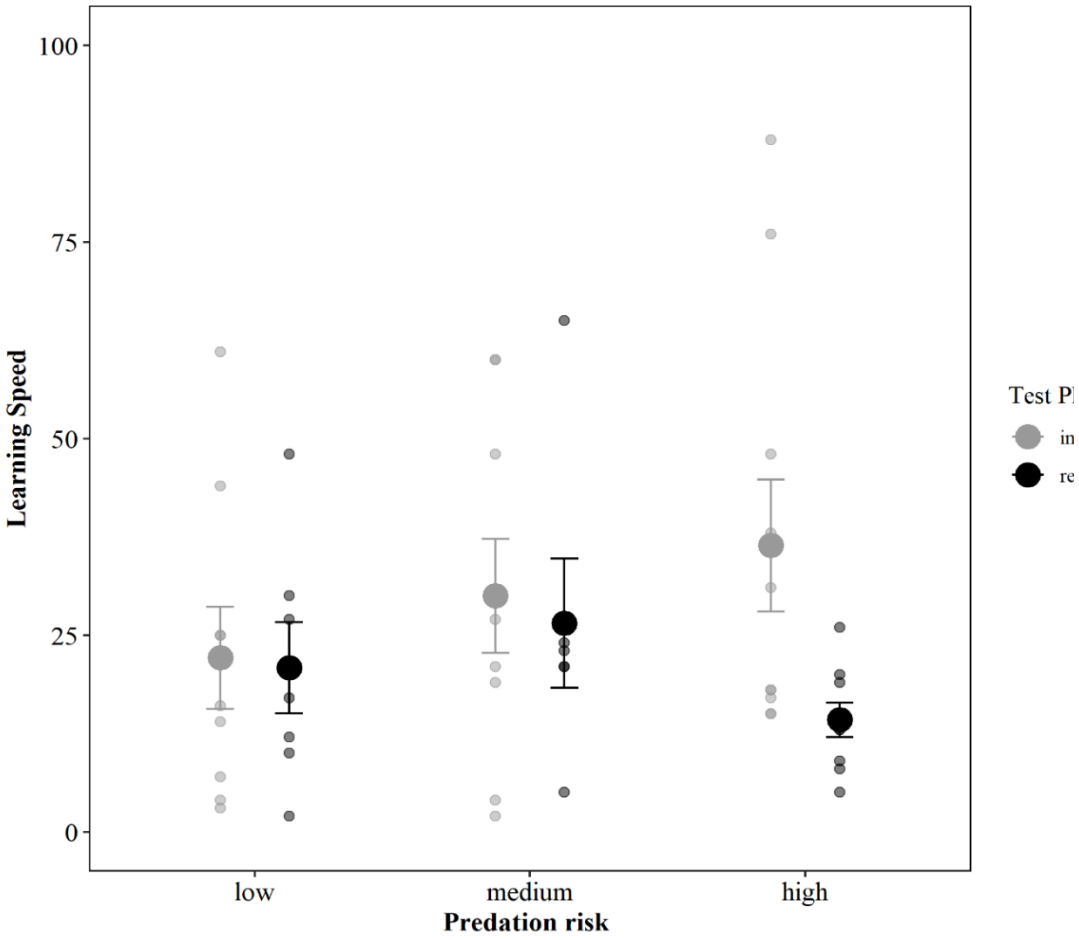

Figure 1. Plot showing the learning speed of both test phases (grey indicates the initial learning speeds and black indicates the reversal learning speeds). Learning criterion was 8/10 correct consecutive visits, and data is categorised into predation risk groups (large dots represent mean ± SE for each combination of trial type (grey, initial learning, n=29; black, reversal learning, n=25) and predator treatment).

Table 1 Full model outputs from the negative binomial generalised linear model with factors affecting initial learning speed (n = 29, d.f. = 23).

explanatory variables	estimate ± s.e.	z	p
intercept	3.16 ± 0.36	8.73	<0.001
treatment (medium)	0.28 ± 0.37	0.75	0.455
treatment (high)	0.51 ± 0.36	1.44	0.150
age[a]	0.14 ± 0.30	0.46	0.643
sex[b]	-0.24 ± 0.30	-0.82	0.412

[a] adult (reference level is juvenile), [b] male (reference level is female). Variables below the dashed line were dropped from the final model, as there was no effect of predation treatment on initial learning speed, the best fit model is the null.

Similarly, I found no effect of predator treatment on reversal learning (see Figure 1 and Table 2). I found that males were faster at reversal learning than females (β = -0.52 ± 0.27 , z = -1.96, p = 0.050; Figure 2, Table 2).

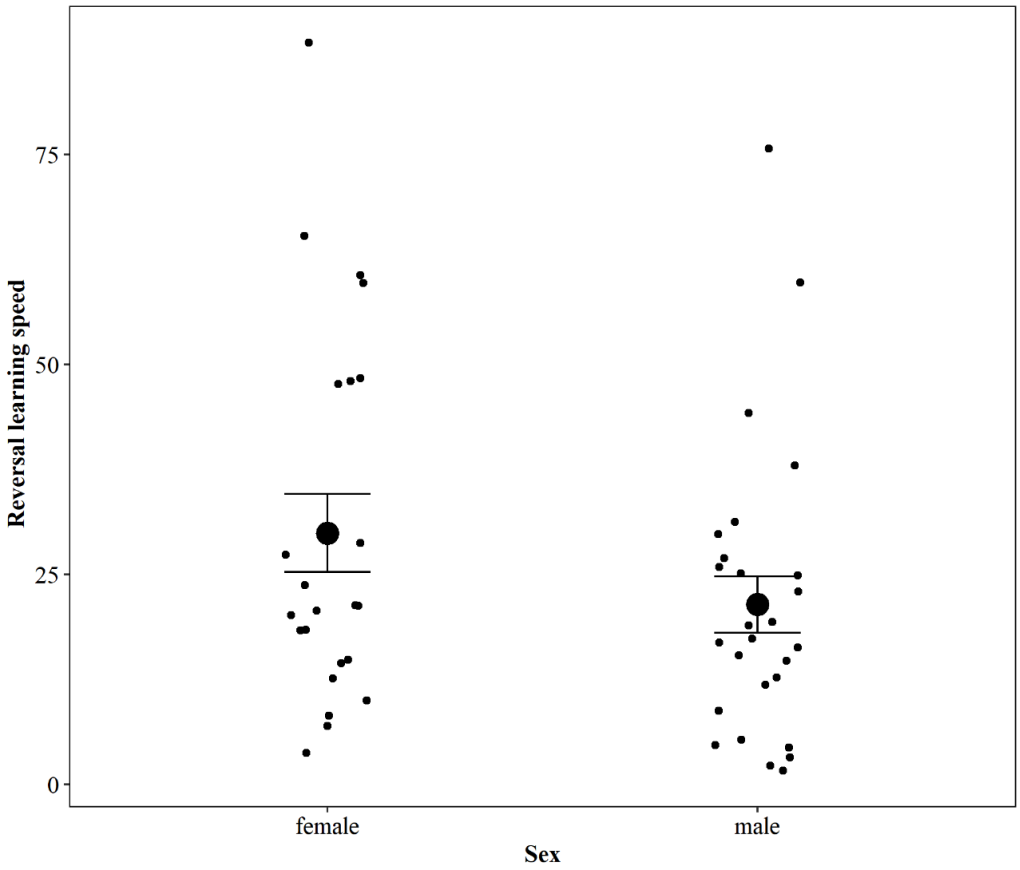

Figure 2. Plot showing the relationship between reversal learning speed and sex. Learning criterion was 8/10 correct consecutive visits, large dots represent mean and the T-bar represents the standard error.

Table 2 Full model outputs from the negative binomial generalised linear model with factors affecting reversal learning speed (n = 22, d.f. = 20).

explanatory variables	estimate ± s.e.	z	p
intercept	3.21 ± 0.19	17.29	<0.001
sex[a]	-0.52 ± 0.27	-1.96	0.050
age[b]	0.37 ± 0.25	1.46	0.140
treatment (high)	0.34 ± 0.29	1.19	0.234
treatment (medium)	0.26 ± 0.32	0.81	0.417

[a] male (reference level is female), [b] adult (reference level is juvenile). Variables below the dashed line were dropped from the final model.

When comparing learning speed between the initial and reverse phases, birds in the high-risk predation treatment had faster reversal learning speeds than initial learning speeds (β =-0.90 ± 0.44, z = -2.11, p = 0.035; Figure 1, Table 3). There was no difference in the reverse and initial learning speed in the medium or low risk groups, between age or sex.

Table 3 Full model outputs from negative binomial generalised linear mixed model of the factors affecting the difference in learning speed across the two trial types (*n* =51 observations of 29 birds).

fixed and random effects	estimate ±s.e.	z	p	variance
intercept	3.01 ± 0.32	9.29	<0.001	
learning phase[a]	0.01 ± 0.33	0.02	0.987	
treatment (medium)	0.34 ± 0.35	0.99	0.324	
treatment (high)	0.58 ± 0.33	1.75	0.080	
age[b]	0.20 ± 0.23	0.90	0.368	
sex[c]	-0.28 ± 0.23	-1.21	0.227	
learning phase[a]*treatment (medium)	-0.16 ± 0.47	-0.34	0.730	
trial type[a]*treatment (high)	**-0.90 ± 0.443**	**-2.11**	**0.035**	

Random effect included bird identity (0.14; 95% confidence interval, CI = 0.12, 0.17) and the residual variance (0.37; 95% CI = 0.30, 0.43). Significant result ($P < 0.05$) is highlighted in bold. [a] reverse (reference level is initial), [b] adult (reference level juvenile), [c] male (reference level is female).

I found a negative correlation between memory and reversal learning speed, where birds with fast learning speeds had poor memory (and vice versa), but only for birds that experienced the high predator treatment (β = -0.24 ± 0.08, z = -2.83, p <0.05, see Figure 3 and Table 4). Memory was not influenced by age or sex.

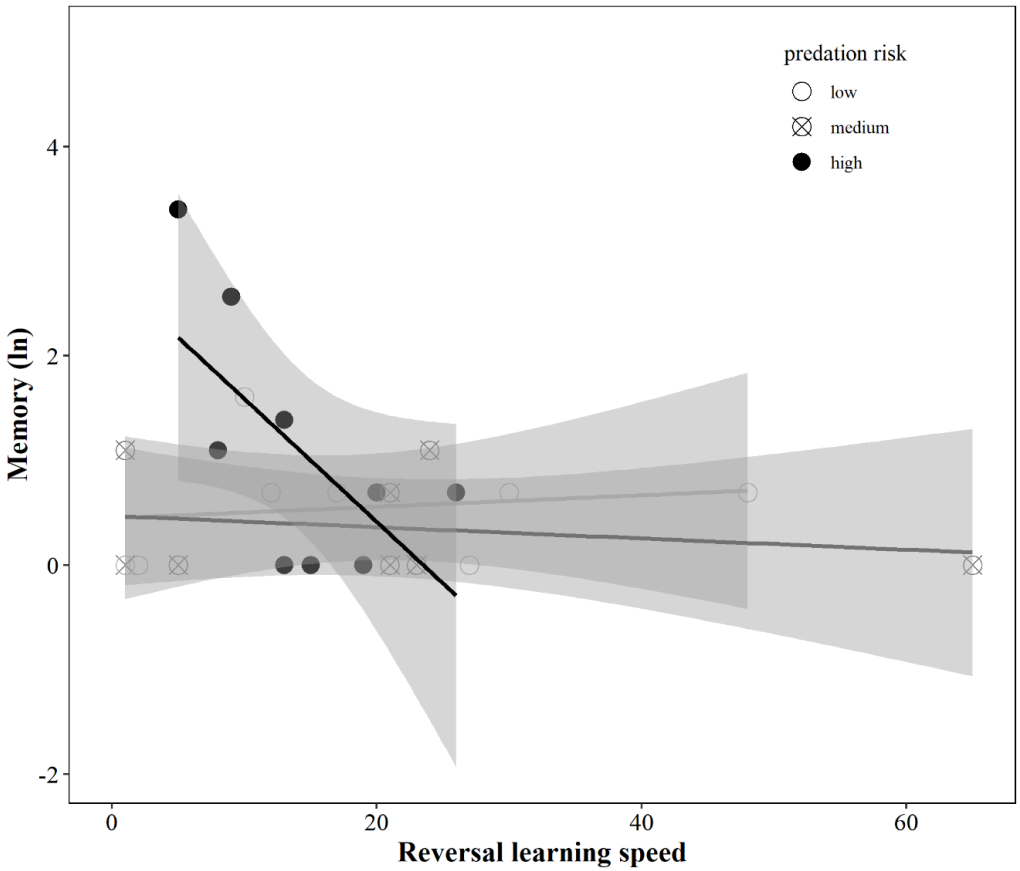

Figure 3. Plot showing the relationship between memory and the interaction between reversal learning speed and predator treatment, where memory is defined as the number of errors before landing on the feeder that was assigned to them during the reversal learning task. (Control n = 8; alarm n = 8, aerial predator n = 9.) Shaded lines show the standard error for each treatment group.

Table 4 Full model outputs from negative binomial general linear mixed model of the factors affecting memory (*n* =25).

fixed and random effects	estimate ±s.e.	t	p
intercept	-0.64 ± 0.84	1.10	0.567
reversal learning speed	0.03± 0.05	0.60	0.56
treatment (medium)	0.17 ± 1.37	0.12	0.903
treatment (high)	4.08 ± 1.13	3.61	0.002
age[a]	-0.95 ± 0.77	-1.26	0.226

sex[b]	0.86 ± 057	1.52	0.147
reversal learning speed*treatment (medium)	-0.03 ± 0.06	-0.42	0.681
reversal learning speed*treatment (high)	**-0.24 ± 0.08**	**-2.83**	**0.012**

[a] adult (reference level is juvenile), [b] male (reference level is female).

Discussion

This study answered three questions concerning the effect of perceived predation risk on cognition. First, I found that the level of predation risk did not affect initial or reversal learning speed, suggesting that cognitive performance is not affected by risk in this context. Second, birds subject to the highest risk of predation performed better in their reversal learning task than initial learning task, however this improved reversal learning speed was not influenced by their initial learning speed. Lastly, birds subject to the highest risk of predation that had a faster reversal learning speed, had relatively poor memory. This effect of memory was not shown for low and medium predation risk. These results suggest that context does matter, and specifically it is the extreme situation of being exposed to an actual predator that induces changes in cognitive performance.

Effects of predation risk on learning speed

Contrary to my prediction I found no difference in spatial learning performance between the different predator treatment groups, both for initial learning speeds and reversal learning speeds. My results from the great tits are in contrast with previous studies in Bischofskarpfling (*Brachyraphis episcopi*), three-spined sticklebacks (*Gasterosteus aculeatus*) and wild guppies (*Poecilia reticulata*), which found predator exposure did affect spatial learning performance (Brown and Braithwaite, 2005; Brydges et al., 2008; Burns and Rodd, 2008). Perhaps our methods of disrupting the foraging behaviour were equally effective across all treatments, resulting in birds foraging not to maximise intake rate, but to maximise safety in all cases. Studies show that flying a model hawk (our high-risk treatment) is an effective method of inducing predator avoidance behaviours in passerine species (Lilliendahl, 1997; Gentle and Gosler, 2001; Voelkl et al., 2016). However, in my experiment, the medium risk

treatment may have been as effective as a visible predator, since birds that forage socially can use both personal and public cues (Templeton and Giraldeau, 1996; Roth et al., 2008), such as conspecific or hetrospecific bird calls. This experiment was carried out during Winter when great tits are known to forage in mixed species groups (Gosler, 1993), thus the alarm calls may have been highly relevant and effective stimuli. However, this does not explain why there was no difference between the high and medium predation risk groups and the low risk group. Alternatively, the lack of difference in learning speeds may be a result of behavioural mitigation regardless of predation treatment due to the individual testing, as solitary individuals are more susceptible to predation and are more likely to be attacked than when part of a group or even group leaders (Ioannou et al., 2019), therefore they may be more likely to exhibit the same predation avoidance behaviour, thus affecting all learning speeds equally. Indeed, previous work on individually tested guppies found predator regime had no effect on the number of errors made in a spatial task (Burns and Rodd, 2008).

I found an effect of sex on reversal learning speed, where males had a faster reversal learning speed than females. I would expect there may be a difference in their abilities, where males would have better abilities than females, because there is greater selective force for males to hold and orientate themselves within their territory (Sherry, 2006). However, I found no evidence of sex differences in initial learning speed or memory. Perhaps they are absent because in the context of this experiment, both males and females are under equal pressure to find food. Furthermore, in great tits, females also need to accurately and efficiently return to their nest and to feeding locations, therefore spatial cognition is important for females too (Sherry, 2006).

Effects of predator treatment on behavioural flexibility

When comparing initial learning speeds with reversal learning speeds within each predation treatment group, I found that birds under the highest predator risk had improved reversal learning speeds when compared to their initial learning speed. Previous work has shown that spatial learning performance improves in response to increased stress (Bednekoff and Balda, 1997; Pravosudov, 2003), potentially due to stress hormones triggering increased physical activity and foraging behaviour (Astheimer et al., 1992; Wingfield, 1997; Breuner et al., 1998; Lynn et al., 2003). There are two potential reasons that stress may have affected performance differently

in the reversal and initial phases, in the high predation risk group. Firstly, the occurrence of high predation risk coupled with the change of reward location could have caused increased stress. Secondly, the accumulation of trials over time, meant that birds experienced consistent and repeated exposure to predation threat which may have resulted in chronic stress (Pravosudov, 2003; Brachetta et al., 2014). Alternatively, they are better able to adjust their behaviour having previously experienced a high predation event (Lima, 2009). Equally, there may have been no increase in stress, and the difference in learning speeds is due to individual experience, causing them to perform differently in reversal learning; the (relatively) slow speed of learning in the high-risk predation group in the initial learning phase, enabled them to acquire more information (Raine and Chittka, 2012; Rowe and Healy, 2014), which they benefited from upon secondary presentation of the task. Finally, the observed differences in spatial learning performance may reflect differences cognitive requirements between the two tasks, i.e. the reversal phase measures behavioural flexibility rather than spatial learning performance (Diamond, 2013; Tello-Ramos et al., 2019). Animals under high stress levels are known to exhibit greater behavioural flexibility (Tello-Ramos et al., 2019); an adaptation for protection (Bolles, 1970; Bonsignore et al., 2008), that can increase survival in unstable environments (Boogert et al., 2010). This frequently manifests in a speed-accuracy trade-off (Brydges et al., 2008; Barou Dagues et al., 2020). In my study, the reversal learning speed was a result of slow initial learning speed coupled with greater cognitive flexibility and high predation pressure, rather than an increase in individual spatial learning ability. Regardless of the exact cause, my result suggests that high predation risk drives adaptiveness in variable environments.

Memory

I found a negative correlation between memory retention and reversal learning speed in the high-risk predation group. If I interpret reversal learning speed as a proxy for behavioural flexibility (as discussed above), then my results support previous studies showing higher levels of behavioural flexibility are associated with reduced memory retention (Tello-Ramos et al., 2019). In a study of mountain chickadees, this effect was most evident at high elevations, which had a harsher climate and poorer foraging conditions (Croston et al. 2016). Notably, in my study this relationship is only evident under high predation pressure, indicating the effect of harsh conditions on memory

and behavioural flexibility is more broadly applicable. Secondly, when interpreting my memory measure, I am assuming that the first visit of each bird is for the purpose of finding food rather than exploration; given the three day retention period, the birds in the high-risk predation group may be exploring the room for predators before they begin to forage.

Conclusion

My study demonstrates that careful observation of spatial learning performance reveals subtle, but important non-lethal predator effects on foraging ecology. I show that predation pressure affects cognitive plasticity and memory. Disentangling whether reduced memory retention in individuals under high pressure arises from causation or correlation remains unknown, thus I suggest further work should investigate this.

Chapter 5. Learning performance is not repeatable in wild mixed flock species due to context-dependent spatial and temporal influences

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Contributions: ACC GLD IGK MSR and JLQ conceived the study. SB and IDLH collected the data. ACC conducted statistical analysis and led the manuscript writing. All authors contributed to interpretation of results and revisions of the manuscript.

Abstract

Foraging is an energetically and cognitively demanding activity that is vital for individual survival. Not only do animals have to search for food, they must also learn and remember when and where to find food, and to update this information as foraging patches change. Learning and remembering about where food is located may depend on spatial and relative positional information, and learning when food is available may depend on temporal information such as circadian and/or sequential cues. However, to date little research has examined how both spatial and temporal information influence foraging efficiency through cognitive processes in the wild. The aim in this study was to examine whether the distance between feeders and the time of day they were rewarding influenced performance and individual consistency across different measures of cognition. In the first experiment, I investigated whether feeder distance affected initial learning, memory and reversal learning. In the second experiment, I tested whether feeder distance influenced temporal learning (the birds' ability to learn when food was available) and reversal temporal learning. This was achieved by assigning one of the feeders in the array available in the morning, and a different feeder available in the afternoon and reversing the feeder locations once they had learned. I found that birds were able to learn, remember and reversal learn where rewarded food was located, regardless of how far apart the feeders were. I also show for the first time in the wild that both great tits and blue tits are capable of temporal and reversal temporal learning. Additionally, I found shorter distances between feeders resulted in faster discrimination learning performance, but had no effect on temporal learning.

Individual characteristics such as age, sex and species variably influenced performance. I found no consistency between the learning performance and reversal learning. Learning performance, as it pertains to foraging, is contextually dependent on distance between foraging patches, as well as individual attributes such as species, sex, and age.

Introduction

Foraging is an energetically and cognitively demanding activity that is vital for individual survival. Ecological variables associated with foraging is thought to drive the evolution of cognition in many species (Rosati, 2017). Animals have to learn and remember when and where to find food (Clayton and Dickinson, 1998), and to update this information as foraging patches change (Johnstone and Dall, 2002). Learning and remembering about where food is located may depend on spatial and relative positional information (Healy and Hurly, 1998), whereas learning when food is available may depend on temporal information such as circadian and/or sequential cues (Feeney et al., 2009). Furthermore, responding to changes in foraging patches may involve different cognitive mechanisms such as value-based decision-making, behavioural flexibility and executive control of responses (Rosati, 2017). Because there may be costs of making mistakes, animals may benefit from learning and remembering information quickly, and therefore I expect learning to be quicker and memory to be better if the cost of making mistakes is higher, if, for example, the distance between potential foraging sites is large. However, the extent to which spatial and temporal information affects learning and memory performance is underexplored. Therefore, the aim of this study was to test the influence of resource layout and availability on multiple cognitive mechanisms and individual consistency in wild mixed species flocks.

Many animals live in complex and unpredictable environments, where they are likely to experience fluctuations in food distribution (Strong and Sherry, 2000; Meltofte et al., 2006; Karell et al., 2009). This uncertainty makes foraging an energetically expensive activity (Hainsworth, 1974), and as a result animals may alter their behaviour to optimise their food intake (Krebs, 1980). The two most important external factors guiding foraging behaviour are where and when food is available (Shettleworth, 2009). To make decisions based on where to find food, animals may

attend to spatial cues (Krebs and Davies, 1987), such as landmarks and landscape features (Cate and Healy, 2017). Animals orientate themselves using abstract cues, such as the distance between landmark features and relative positional cues (Gallistel, 1990). Foraging decisions are also influenced by distance to predator-concealing cover or edge effects, (Whittingham et al., 2004; Cresswell et al., 2010), as well as the relative position of a foraging patch (Reichert et al., 2020). Whereas decisions based on when to search for food, are prompted by circadian rhythm (defined as the internal processes synchronised to the 24hr cycle in external time cues, i.e. light and temperature (Edery, 2000) and sequential cues (i.e. order) (Richelle et al., 2013). These cues can be used simultaneously by learning a sequence of reoccurring daily events, and linking this information to a circadian rhythm (Shettleworth, 2009). In addition, foraging decisions are also influenced by internal or individualistic factors such as hunger state (Croy and Hughes, 1991), personality (Aplin et al., 2014), reproductive state (Geary et al., 2020), age and sex (Patrick and Weimerskirch, 2014). For example, in wild chacma baboons (*Papio ursinus*) foraging strategy is correlated with personality, where bold individuals are foragers, while shy individuals scrounge (Carter et al., 2013b); black-legged kittiwakes (*Rissa tridactyla*) can adjust their foraging behaviour based on their body condition and chick age (Christensen-Dalsgaard et al., 2018). To strike the right balance between energy expenditure and intake, many animals mediate their feeding-related behaviour via cognition (Johnstone and Dall, 2002); however to date, there has been little research into the role of spatial and temporal variation influencing cognitive performance of foraging in the wild.

When animals move throughout their environment, they must engage multiple cognitive mechanisms (Rosati, 2017). First, animals must learn to discriminate, which is a two-stage process; learning what stimulus to attend to, and learning how to respond (Sutherland and Mackintosh, 2016). Discrimination learning allows animals to distinguish between edible and inedible prey items (Lindström et al., 1999), relative value of edible items (Kulahci et al., 2008), and productive and unproductive food patches (Krebs, 1980). Second, animals must remember this information and use it to guide future behaviour (Shettleworth, 2009). Many species (e.g. European nuthatch (*Sitta europaea*) (Källander, 1993), red squirrel (*Sciurus vulgaris*) (Wauters et al., 1995), Pygmy Owls (*Glaucidium passerinum*) (Solheim, 1984)) will cache food in multiple locations in order to survive in harsh or unpredictable environments (Brodin,

2010). However, even for non-hoarding species, food sources and site productivity change over time due to seasonal changes and fluctuation in prey items (Krebs and Davies, 1987), or density of conspecifics (Krebs, 1980). For example, white-faced saki monkeys (*Pithecia pithecia*) are known to follow sub-optimal routes between sites, which enables them to assess the abundance and maturation of other fruit trees (Cunningham and Janson, 2007), thus the immediate cost in energy in visiting non-rewarding sites is later balanced when the fruit ripens. The assumption here is that animals must learn where they have found food and when it is available, remember this information and update it as it changes, and therefore cognitive mechanisms that augment flexible behaviour are like to be beneficial. However, the nature of the information, such as the relative distance between foraging sites may influence how well individuals learn, remember and update this information, perhaps due to differences in the cost of making mistakes. Therefore, I investigated how spatial and temporal information affected learning, memory and reversal learning in a mixed species flock of wild birds.

In this study, I used arrays of four feeders across six different woodland sites where each feeder could be programmed to restrict or allow individual access depending on the location and time of day. The aim was to examine whether the distance between feeders influenced performance and individual consistency across different measures of discrimination learning. At three sites, feeders were positioned one metre apart (low energetic cost of learning), and at the other three sites, the feeders were spaced three metres apart (high energetic cost of learning). I assumed that making errors at feeders that were positioned three metres apart would be more energetically costly than errors made at feeders positioned one metre apart and therefore there would be more of an incentive for birds to perform better at sites where feeders were more widely spaced. In the first experiment, I investigated whether feeder distance affected initial learning, memory and reversal learning performance. In the second experiment, I tested whether birds could learn a temporal association, and whether feeder distance influenced learning speed by assigning one of the feeders in the array to be available in the morning, and a different feeder to be available in the afternoon. Finally, in a temporal reversal task, I switched the feeder that was rewarded in the morning to be rewarded in the afternoon, and vice versa. I also predicted that there may be differences in performance between species, and differences within species according to age and sex.

Lastly, I examined whether individual performance was repeatable across my learning measures, as this may provide evidence that performance across different aspects of discrimination learning is measuring an inherent (cognitive) trait common among all tasks.

Methods

Study site and species

The study took place at six sites (minimum separation distance 2km) in the Bandon Valley, County Cork, Ireland from November 2018 to February 2019. Five of the sites were mixed deciduous and one site was a conifer plantation. Birds were captured with mist nets and ringed with a unique metal British Trust for Ornithology (BTO) ring, aged and sexed via their feathers. Great tits and blue tits were additionally fitted with plastic rings containing a passive integrative transponder (PIT) tag (IB Technology Aylesbury, UK), allowing for individual identification of birds that interacted with the experimental devices (see below).

Feeder array

At each of the six sites, I set up one feeder array, consisting of four linear aligned feeders. Each feeder was filled with sunflower seeds (*Helianthus annuus*). The proximity of parallel cover (e.g. hedges) necessitated a linear feeder array, as distance from cover affects performance (Morand-Ferron and Quinn, 2011). The spacing of feeders within each array was randomly assigned according to distance treatment; at three sites, feeders were positioned 1 m apart, while at the other three sites, feeders were positioned 3 m apart from each other. In order to be able to robustly statistically analyse the effect of distance between feeders I required a sample size of at least three per treatment (1 m or 3 m). To save battery life, feeders were activated automatically each day from approximately 30 min before sunrise to approximately 30 min after sunset (the time changed throughout the season to match daylight hours and was checked each time the battery was changed). Each feeder was equipped with a radio frequency identification (RFID) antenna placed near the single opening to the feeder, which served as a perch and recorded the individual PIT tag and time of visit for each bird on the perch. To protect feeders from damage caused by mammals and larger birds, feeders were enclosed by a cylindrical cage of 31mm wire mesh, large enough for the tits to pass through.

When birds were assigned their rewarded feeder, access to food was controlled by a solenoid placed behind a transparent plastic door at the feeder opening (Reichert et al., 2020). The solenoid would release if a specific pre-programmed PIT tag was detected. Once the solenoid was released, birds had access to the food behind the door (see below) (Reichert et al., 2020). RFID readings and solenoid activation were controlled by a custom program loaded onto a printed circuit board ('Darwin Board', Stickman Technologies Inc., UK) (Reichert et al., 2020). Visits were monitored with the RFID antenna throughout the experiment.

Learning Experiment

To attract and habituate birds to the feeder arrays prior to the learning experiment, all feeders were open and accessible to all birds for 18 days: for 9 days all birds had access to all of the feeders (23 Nov – 2 Dec 2018). For the following 9 days, the feeders were programmed to open when any PIT tag was detected so only tagged birds had access to all of the feeders (2-11 Dec 2018).

To measure individual variation in learning performance, I restricted each individual's access to only one of the four feeders, by programming the particle control board with a list of randomly assigned PIT-tagged birds. Hence, each feeder would only open to allow access to food for specified birds, while recording visits from all the birds.

The first experiment was set up in three phases: 1. the initial discrimination learning phase, 2. the memory phase, 3. the discrimination reversal learning phase (see below for learning criteria). For the initial discrimination learning phase, each bird was randomly allocated to be rewarded at only one of the four feeders (trial lasted 8 days 11-19 Dec 2018), and they had to learn which of the four feeders was their assigned feeder. Birds were not assigned to their preferred feeder (i.e. the feeder they visited most in the habituation phase). The learning speed was calculated as the number of visits until birds reached criterion, defined as visiting the correct feeder 80% of the time on 20 consecutive visits with the requirement that the first of the 20 visits be to the correct feeder (Reichert et al., 2020). After a 27-day retention period (where feeders were removed), the birds took part in a memory phase, where only the initial feeder was rewarding. Memory was quantified as the number of visits until they first visited their initial rewarded feeder (trial lasted 8 days, 15-23 Jan 2019). Immediately following the memory phase, birds took part in a discrimination reversal learning

phase where each bird was assigned to a new feeder, and the learning speed was calculated as above (trials lasted 8 days, 23-31 Jan 2019).

In the second experiment, there were two phases, 1. the temporal learning phase and 2. the reversal temporal learning phase. In the temporal learning phase, the feeders were programmed to alternate rewarded feeder location where they could access their assigned feeder from the reversal learning experiment in the morning (08:00 to 11:59) and their (previously rewarded) initial feeder in the afternoon (12:00 to 17:20) (trials lasted 10 days, 31 Jan-10 Feb 2019). I considered birds to have learned the task once they had met the criterion of visiting the correct feeder in 8 out of 10 consecutive visits in the afternoon and 8 out of 10 consecutive visits in the subsequent morning with the first visit in the morning being to the correct feeder. I quantified learning speed as the number of half day (i.e. morning and afternoon) periods until birds reached the "successful" morning period that was preceded by a "successful" afternoon period. Finally, in the temporal reversal learning phase, I reversed the order of the feeders, such that the initial learning feeder was rewarded in the morning and the reversal feeder was rewarded in the afternoon (trials lasted 10 days, 10-20 Feb 2019). Learning speed was calculated in the same way as the initial temporal learning phase.

Visits and data inclusion

The raw dataset consisted of rows containing the date, time and PIT tag for each detected visit at each feeder. I considered consecutive detections of the same bird to the same feeder within two seconds of each other to be a single visit (Evans et al., 2018). Birds had to visit the feeders at least 20 times per phase (hereafter participated) to be included in the analysis, as this was the minimum visits required for the calculation . To account for previous experience, and to insure that I was testing reversal learning performance, only birds that reached criterion in the previous phase were included in the analysis of the following phase (i.e. birds had to reach criterion in each phase to continue in the experiment). There was wire mesh surrounding each device, which provided ample space for perching, therefore I assumed that each visit was an attempt to feed, and I counted each visit to an unassigned feeder as an error, and each visit to the assigned feeder as a correct choice (Reichert et al., 2020). Similarly to Reichert et al. (2020), several feeders malfunctioned during the experiment and did not open for any of the birds or record any visits until they were

repaired. Malfunctions occurred either because of failure of the antenna to register any visits or unexpected loss of power to the devices. I therefore included the duration of feeder malfunction before the bird reached learning criterion for both the assigned (own) feeder and separately for any of the other feeders in that site as additional fixed effects.

Statistical analysis

For the following five analyses, I ran separate general linear mixed models (GLMMs), where the response variable was the cognitive measure from each of the phases and feeder array site was the random term. Initially I carried out the GLMMs with a Poisson distribution, which revealed (in each case) an overdispersion statistic of >2. Therefore, each response variable was log-transformed to meet assumptions of normality and analysed using GLMM with a Gaussian distribution. I chose the log-transformed Gaussian fit model over a negative binomial GLMM because the model validation checks indicated that model assumptions were better met using the former model. I used R v. 4.0.3 software (R Core Team, 2020) to fit an initial model and performed a backwards stepwise selection of non-significant terms starting with the non-significant interaction, comparing consecutive models using the Akaike's information criterion (AIC) and likelihood-ratio tests to determine the model with the best fit.

For all models in the discrimination experiment, I included feeder distance (1 m or 3 m), species (blue tit or great tit), age (adult or juvenile), position of feeder in the array (centre or edge), rewarded feeder malfunction duration, and non-rewarded feeder malfunction duration as fixed effects. After basic plotting of the data, I decided to include the interaction between species and feeder distance, to account for differences in learning performance between the two species. Additionally, in the reversal discrimination model I included a three-way interaction (Initial learning speed*Species*Distance), to account for any carry-over experience from the initial phase on the learning performance between the two species. The variable sex (female, male or unknown) was highly colinear with species (great tit or blue tit), because blue tits are sexually monomorphic in the winter. In order to maintain the sample size and explore the full dataset I excluded sex as a variable in my analyses, however I repeated

the models described below on great tits only in order to explore sex differences in my experiment (N = 55; male = 31, female = 24).

For the two models from the temporal experiment, I included the factors listed above, with the exception of feeder position, which was reclassified to reflect the change in distance to cover of the rewarded feeder between the morning and afternoon periods (centre for both periods, different or edge for both periods). In the reversal temporal learning, initial temporal learning speed is also included. I did not include the three-way interaction from above as there were convergence issues, due to the smaller small size of the reversal temporal dataset.

Finally, I examined individual consistency in initial and reversal learning performance in the discrimination and in the temporal experiments, in four subsets based on spacing of feeder array (1 m or 3 m) and species (great tit and blue tit). Using the rptR packing (Stoffel et al., 2017), I determined individual repeatability (hereafter consistency) by estimating repeatability (intra-class correlation) and confidence intervals (C.I.) in each of the two experiments. I used the log-transformed learning speed with a Gaussian distribution (Stoffel et al., 2017), and included experimental phase (initial or reversal), distance (1 m or 3 m), species (great tit or blue tit), age, sex, position of feeder, own feeder malfunction and other feeder malfunction as fixed variables. I report unadjusted and adjusted repeatability, to encompass repeatability before and after controlling for influential fixed effects (Cauchoix et al., 2018). For both adjusted and unadjusted repeatability, I included individual identity as a random effect. To account for multiple comparisons, I corrected the p-values for multiple comparisons. I report corrected p-values in the text, and I include the uncorrected p-values in the table 7.

Results

Of the 147 individuals that visited the feeders (great tits (n = 68) and blue tits (n = 79)) across all phases of the experiment at the six different field sites, 142 individuals visited at least 20 times per phase and were included in the analysis. A summary table of the numbers of individuals that a) participated in, b) learned, c) learned and met criteria in the previous phase (i.e. were included in the analysis) can be found in Table 1.

Table 1 Summary of descriptive statistics for all phases of the experiment

	Participated	Learned	Learned and met criteria in previous phase	Min	Median	Mean	Max
Initial learning	142	126	NA	1	6	19.62	550
Memory	118	93	92	1	2	7.36	346
Reversal learning	97	95	92	1	10	12.31	47
Temporal initial learning	104	66	63	2	4	6.29	18
Temporal reversal learning	94	55	43	2	5	7.36	19

The min, median, mean and max values are based on learning speeds; for the discrimination experiment the figures represent number of visits, and for the temporal experiment the figures represent the number of am/pm periods before reaching criterion.

Experimental Phases

In the initial learning phase, I found a significant interaction between species and the spacing between the feeders (β = 1.39 ± 0.44, t = 3.14, p = 0.002; figure 1(a), table 2). Great tits assigned to the 1 m spaced array learned faster than great tits assigned to the 3 m spaced array but there was no effect of feeder distance on learning speed in blue tits. Across both species, adults learned faster than juveniles (β = 0.59 ± 0.24, t = 2.45, p = 0.016; figure 1(b), table 2). Individuals assigned to an edge feeder learned faster than those assigned a centre feeder (β = -0.47 ± 0.23, t = -2.06, p = 0.041; figure 1(c), table 2). Individuals tended to have slower learning speed if their assigned feeder malfunctioned (β = 0.11 ± 0.06, t = 1.78, p = 0.079; table 2) and had slower learning speed if a non-rewarding feeder malfunctioned (β = 0.07 ± 0.03, t = 2.06, p = 0.041; table 2). In the analysis conducted on great tits only, I found no sex differences in initial learning speed (table A1).

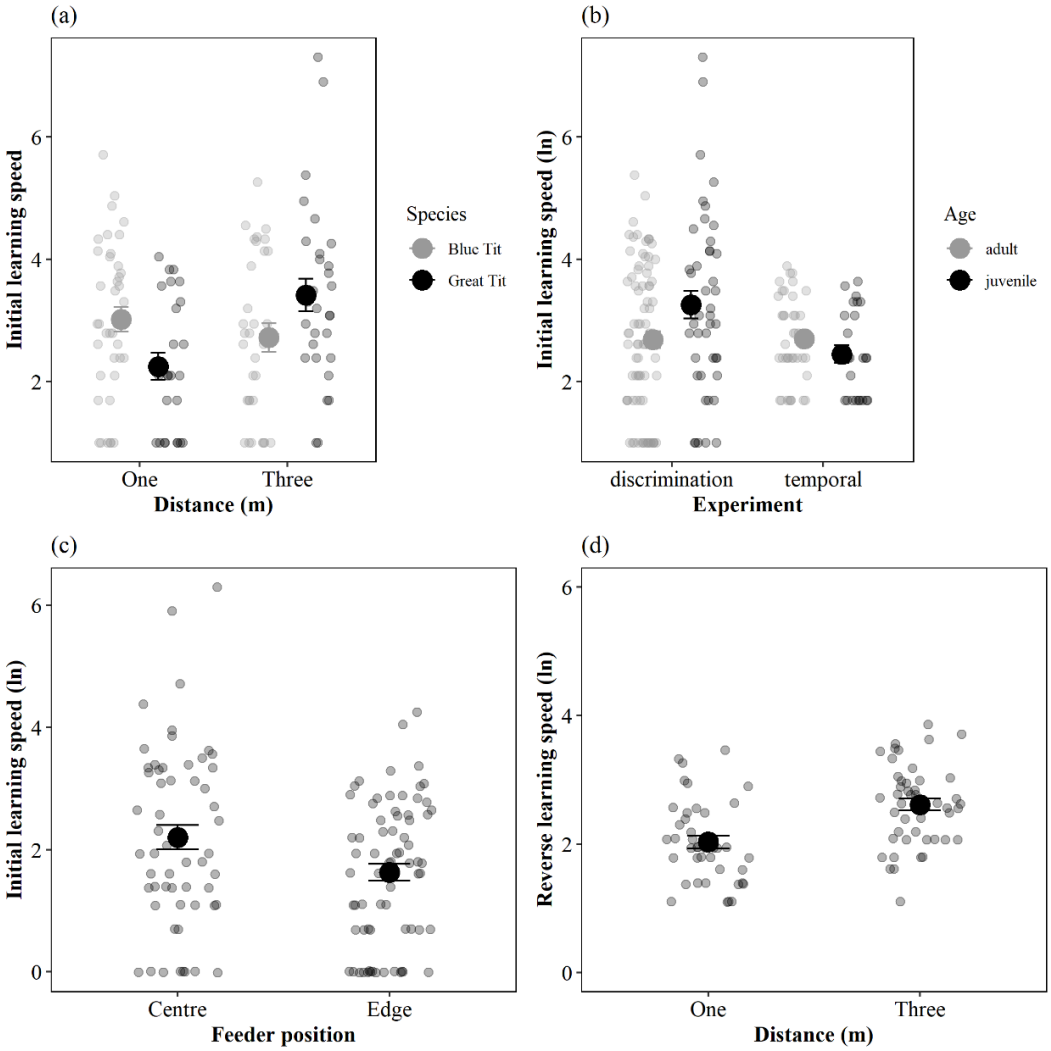

Figure 1. For all graphs, lower y-values represent faster learning, where small data points represent individual birds (points have been jittered along the x-axis), and the large point represents the mean and the t-bars represent the standard error of the mean. (a) The interaction between species and feeder spacing on initial learning speed. Learning speed is the number of visits to criterion. The light grey points represent birds assigned to a 1 m feeder array, while the dark grey dots represent birds assigned to a 3 m feeder array. (b) The effect of age on initial discrimination and initial temporal learning speed. Adults are birds that had experienced a breeding season, whereas juveniles had not. (c) The effect of feeder position on initial discrimination learning. (d) The effect of feeder spacing array on reversal learning speed. Lower values represent faster learning. Birds were assigned to one of two treatments, an array where feeders were spaced by 1 m or 3 m.

Table 2 Full model output from the general linear model with factors affecting initial learning speed (n = 126, d.f. = 114).

Term	Coefficient	Standard error	Z	P
Intercept	3.051	0.288	10.58	<0.001
Distance[a]	-0.459	0.381	-1.21	0.294
Species[b]	-0.809	0.316	-2.564	0.012
Age[c]	**0.588**	**0.240**	**2.446**	**0.016**
Own feeder malfunction	0.114	0.064	1.775	0.079
Other feeder malfunction	**0.069**	**0.034**	**2.050**	**0.043**
Feeder array position[d]	**-0.467**	**0.226**	**-2.064**	**0.041**
Distance[a]*species[b]	**1.394**	**0.444**	**3.141**	**0.002**

[a] three metres (reference level one metre), [b] great tit (reference level is blue tit), [c] adult (reference level is juvenile), [d] edge (reference level is centre)

In the memory phase, I found that none of my fixed variables explained the variation in memory (see table 3). In the analysis conducted on great tits only, I found no sex differences in memory (table A2). However, a Wilcoxon 1-sample test showed that birds performed better than chance showing that they did remember their previously rewarding feeders four weeks later (where mu = 0.25; p = <0.001).

Table 3 Full model output from the general linear model with factors affecting memory (n = 87, d.f. = 81). Terms above the dashed line are retained in the minimum adequate model.

Term	Coefficient	Standard error	Z	P
Intercept	1.191	0.109	10.912	<0.001
Distance[a]	-0.182	0.150	-1.215	0.291
Species[b]	-0.122	0.169	-0.718	0.475
Age[c]	-0.180	0.119	-1.513	0.135
Initial learning speed	0.000	0.000	0.267	0.791
Feeder array position[d]	0.0354	0.112	0.315	0.754
Own feeder malfunction	-0.022	0.037	-0.593	0.555
Other feeder malfunction	0.005	0.020	0.271	0.787
Distance[a]*species[b]	0.277	0.230	1.205	0.232

[a] three metres (reference level one metre), [b] great tit (reference level is blue tit), [c] adult (reference level is juvenile), [d] edge (reference level is centre)

During reversal learning, individuals from both species learned faster on the 1 m spaced feeders, compared to the 3 m spaced feeders (β = 0.57 ± 0.16, t = 3.50, p = 0.025; figure 1(d), table 4). Great tits tended to reversal learn faster than blue tits (β = -0.27 ± 0.14, t = -1.95, p = 0.055; table 4). Birds had slower learning speeds when their assigned feeder malfunctioned (β = 0.09 ± 0.04, t = 2.18, p = 0.032; table 4), and when non-rewarding feeders malfunctioned (β = 0.07 ± 0.03, t = 2.16, p = 0.034; table 4). Reversal learning speed was unaffected by initial learning speed, memory, age, or feeder position within the array. In the analysis conducted on great tits only, there was a non-significant trend for males to reversal learn more slowly than females (β = 0.35 ± 0.18, t = 1.88, p = 0.072; table A3).

Table 4 Full model output from the general linear model with factors affecting reversal learning speed (*n* = 87 d.f. = 78). Terms above the dashed line are retained in the minimum adequate model.

Term	Coefficient	Standard error	Z	P
Intercept	2.088	0.120	17.382	<0.001
Distance[a]	**0.571**	**0.163**	**3.500**	**0.025**
Species[b]	-0.267	0.137	-1.948	0.055
Own feeder malfunction	**0.093**	**0.0427**	**2.178**	**0.032**
Other feeder malfunction	**0.071**	**0.0298**	**2.394**	**0.019**
Initial learning speed	0.008	0.005	1.617	0.110
Memory	0.002	0.002	1.166	0.248
Age[c]	0.053	0.145	0.363	0.718

Feeder array position[d]	-0.167	0.140	-1.198	0.235
Distance[a]*species[b]	-0.149	0.384	-0.388	0.699
Initial learning speed*Species[b]	-0.022	0.027	-0.835	0.407
Initial learning speed*Distance[a]	-0.021	0.009	-2.260	0.027
Initial learning speed*Species[b]*Distance[a]	0.035	0.028	1.271	0.208

[a] three metres (reference level one metre), [b] great tit (reference level is blue tit), [c] adult (reference level is juvenile), [d] edge (reference level is centre)

In experiment 2, the initial temporal learning phase, juveniles learned faster than adults ($\beta = -0.40 \pm 0.17$, $t = -2.38$, $p = 0.02$; figure 1(a), table 5). Birds had faster learning speeds when non-rewarding feeders malfunctioned ($\beta = -0.05 \pm 0.01$, $t = 3.88$, $p < 0.001$; table 5). I found no effect of distance between feeders, species, or feeder position within the array. In the analysis conducted on great tits only, I found no sex differences in temporal learning performance (table A4).

Table 5 Full model output from the general linear model with factors affecting temporal learning speed ($n = 63$, d.f. = 55). Terms above the dashed line are retained in the minimum adequate model.

Term	Coefficient	Standard error	Z	P
Intercept	2.623	0.1	26.27	<0.001
Age[a]	**-0.395**	**0.166**	**-2.381**	**0.02**

Other feeder malfunction	**0.051**	**0.013**	**3.881**	**<0.001**
Distance[b]	-0.097	0.224	-0.432	0.668
Species[c]	0.463	0.349	1.327	0.19
Feeder array position[d] (different)	-0.006	0.347	-0.016	0.987
Feeder array position[d] (edge)	0.09	0.401	0.226	0.822
Own feeder malfunction	0.028	0.028	0.989	0.327
Distance[a]*species[c]	-0.291	0.407	-0.714	0.478

[a] adult (reference level is juvenile),[b] three metres (reference level one metre), [c] great tit (reference level is blue tit), [d] different or edge (reference level is centre)

In the reversal temporal phase, I found no effect of my experimental treatment or biologically relevant factors (see table 6). Birds tended to learn more slowly the more their rewarded feeders were malfunctioning ($\beta = 0.23 \pm 0.12$, $t = 1.88$, $p = 0.069$; table 6) and learned more slowly if any of the other feeders were malfunctioning ($\beta = 0.08 \pm 0.02$, $t = 4.47$, $p < 0.001$; table 6). In the analysis conducted on great tits only, I found an effect of sex, where males were faster at temporal reversal discrimination learning than females ($\beta = -0.64 \pm 0.20$, $t = -3.15$, $p = 0.008$; figure A1, table A5).

Table 6 Full model output from the general linear model with factors affecting temporal reversal learning speed (n = 43, d.f. = 35). Terms above the dashed line are retained in the minimum adequate model.

Term	Coefficient	Standard error	Z	P
Intercept	2.549	0.108	23.627	<0.001
Own feeder malfunction	0.233	0.124	1.878	0.069
Other feeder malfunction	**0.076**	**0.017**	**4.467**	**<0.001**
Distance[a]	0.195	0.278	0.703	0.521
Temporal learning speed	-0.004	0.023	-0.173	0.864

Species[b]	0.041	0.496	0.082	0.935
Age[c]	0.131	0.201	0.652	0.520
Feeder array position[d] (different)	-0.404	0.416	-0.971	0.340
Feeder array position[d] (edge)	0.290	0.492	0.588	0.561
Distance[a]*Species[b]	-0.431	0.552	-0.781	0.441

[a] three metres (reference level one metre), [b] great tit (reference level is blue tit), [c] adult (reference level is juvenile), [d] edge (reference level is centre)

Repeatability of learning speeds

I found no consistency in learning performance across the discrimination or temporal experiments in birds assigned to the 1 m spaced feeding array, in birds assigned to the 3 m spaced array, in great tits only (both spacing arrays) and in blue tits only (both spacing arrays) (table 7).

Table 7 Repeatability (adjusted and unadjusted) estimates for learning speed during all four phases of the experiment. Unadjusted values are from mixed models with only individual as a random effect. Adjusted values also include fixed effects.

model	**repeatability**	**r**	**standard error**	**confidence interval (lower, upper)**	**P (corrected for multiple comparisons)**
Distance (1m)					
Initial and reversal discrimination learning	adjusted	0.098	0.144	0, 0.486	1
	unadjusted	0.137	0.126	0, 0.417	1
Temporal initial and temporal reversal	adjusted	0	0.269	0, 0.864	1
	unadjusted	0	0.175	0, 0.582	1
Distance (3m)					
Initial and reversal discrimination learning	adjusted	0	0.110	0, 0.358	1
	unadjusted	0.063	0.103	0, 0.342	1
Temporal initial and temporal reversal	adjusted	0.156	0.161	0, 0.578	1
	unadjusted	0	0.103	0, 0.338	1
Great tit only					
Initial and reversal discrimination learning	adjusted	0.178	0.162	0, 0.603	1
	unadjusted	0.376	0.147	0.039, 0.626	0.216
Temporal initial and temporal reversal	adjusted	0.081	0.200	0, 0.670	1
	unadjusted	0	0.126	0, 0.411	1

Discussion

I found that birds were able to learn, remember and reversal learn where rewarded food was located (table 8). I also report for the first time that both great tits and blue tits are capable of temporal and reversal temporal learning in the wild. Additionally, I found shorter distances between feeders resulted in faster discrimination learning performance, but had no effect on temporal learning. Adults learned the initial discrimination task faster than juveniles; however juveniles outperformed adults on the initial temporal learning task. When examining sex differences (in the subset of great tits only), I found that females tended to reversal learn faster than males, however males outperformed females on the temporal reversal task. Moreover, I found no evidence of individual performance consistency with the discrimination experiment or the temporal experiment. I discuss the implication of these differential effects across the two cognitive experiments.

Table 8 Summary of the relationships between cognitive task and fixed effects

Fixed effects	Initial discrimination learning	Memory	Reversal discrimination learning	Initial temporal learning	Reversal temporal learning
Distance	NS	NS	(-) 3 m	NS	NS
Species	(+) great tit	NS	NS	NS	NS
Age	(-) juvenile	NS	NS	(+) juvenile	NS
Own feeder malfunction	NS	NS	(-)	NS	NS
Other feeder malfunction	(+)	NS	(-)	(-)	(-)
Feeder array position	(+) edge	NS	NS	NS	NS
Distance*species	(+) great tit, 1 m	NS	NS	NS	NS
Initial discrimination learning speed	NA	NS	NS	NA	NA

Feeder distance

Feeder distance affected discrimination learning performance, but not temporal learning performance or memory. In contrast to my predictions, performance on both discrimination tasks was better at the 1 m feeder arrays. During the initial discrimination task, great tits assigned to the 1 m feeding array demonstrated faster learning performance, and both species had faster reversal learning performance at the 1 m arrays. This effect could have arisen for many reasons. First, birds may have learned the position of their rewarding feeder in relation to the other feeders in the array, using geometric relations (i.e. retinal snapshots) (Collett et al., 1986). If great

tits and blue tits rely on retinal snapshots to learn where rewarding feeders are positioned relative to other feeders in the array, then a smaller spacing between feeders may have facilitated retinal snapshots that encompassed the full array. In contrast, the 3 m arrays may have precluded birds from learning using this navigational mechanism, and therefore may have had to rely on larger, global cues to remember the location of rewarding feeders. Second, the difference in learning speed may be due to flock density. The proximity of other flock members as a result of the closely spaced feeding array, potentially provided safety and extra vigilance for those birds, which facilitated better learning performance; while at the 3 m feeder arrays, the spread of the flock was increased three-fold, requiring them to spend more time being vigilant than attending to information about where and when feeders were rewarding. In contrast, previous learning experiments which use automated feeders, cite interference from conspecifics (Croston et al., 2016), as well as increased error visits to neighbouring feeders (Reichert et al., 2020), as evidence of reduced learning performance, indicating that proximity to neighbours hinders learning. Therefore, future work could involve social network analysis to investigate the effect of density flock density on learning performance.

Temporal learning

Results from the temporal experiment demonstrate, for the first time, that great and blue tits are capable of learning when food is available in specific locations, and that these birds can adjust their behaviour to meet changing temporal contingencies. For great tits and blue tits, peak abundances of plant and invertebrate foods occur at different times, daily and seasonally (Gosler, 1993); therefore, understanding when food is available is advantageous, and may be subject to natural selection (Darwin, 1871). The lack of effect of feeder distance in the temporal learning experiment, is possibly due to the task being too complex, meaning the challenge of feeder distance was overshadowed by the complexity of timing during the experiment. Furthermore, a lower percentage of birds completed the initial temporal task compared to the discrimination task, indicating that in general, learning "when" may be more difficult than learning to discriminate, (63% compared to 87%; see Table 1). Difficulty in learning the "when" component of the task is evident in rodents (Bird et al., 2003), birds (Marshall et al., 2013) and primates (Hampton et al., 2005), possibly because it is more abstract than the physical "what" and "where", and without ecological

relevance, it may not have evolved (Clayton and Dickinson, 1998). However, the percentage of birds capable of temporal learning is similar for reversal temporal phase (63% compared to 58%; see Table 1), indicating that learning when food is available, is as difficult as adjusting ones' behaviour according to when food is available. Moreover, the second component of the temporal task demonstrates that blue and great tits are capable of linking separate concepts, such as alternating feeding locations in conjunction with the time of day, to make informed foraging decisions. Additionally, I found evidence that individual characteristics play a role in temporal learning. Males in my study, showed a greater degree of behavioural flexibility in a temporal context, which contrasts with previous studies on behavioural flexibility in fish (Reader and Laland, 2000; Lucon-Xiccato and Bisazza, 2014). One hypothesis for sex differences in behavioural flexibility involves mating roles, where it would be beneficial for males to be persistent (Rowe et al., 2005), therefore it is not clear why I found opposing results. However, the link between sex and cognition does appear to be context dependent, because in the discrimination experiment there was a trend for females to behave more flexibly.

Individual characteristics (Species differences and age)

I tested birds' ability to locate food sites across multiple iterations of the experiments, but I did not account for competition and dominance effects, nor did I account for predation, both of which may influence the learning performance of the birds. Trapanese et al., (2019) state that animals must overcome three obstacles while foraging, i) locating scattered food sites, ii) competition from others, and iii) predation. The patterns in learning performance across both species and age (and trend in sex) are potentially explained by competition and dominance, where blue tits are subordinate to great tits (Dhondt and Eyckerman, 1980; Kempenaers and Dhondt, 1991) and juveniles are subordinate to adults (Sandell and Smith, 1991; Sol et al., 1998). Both great tits and adults may have been displacing subordinates at the devices, and consequently outperformed their subordinates in the initial discrimination learning task. However, once they were presented with a more complex task (i.e. reversal learning and temporal learning), the species difference disappeared, while the age differences reversed. This suggests that the blue tits or juveniles may have explored the array more extensively when they were displaced in the previous phase. More broadly, my results suggest that subordinate individuals who were more flexible,

eventually ended up with similar or exceeded performance as a result of earlier exploration. Future work could compare the displacements at feeders and compare sampling strategies across different species, age and sexes, including the visits after they have knowledge of rewarding locations.

Behavioural consistency

I found no evidence of consistency in learning performance in either the discrimination or the temporal experiment. Previous research has attributed error visits as interference from others near the rewarded feeder (Croston et al., 2016). However, my data show that even at widely spaced feeders, where competition and interference are likely reduced, I still find a lack of consistency within the discrimination and temporal measures. My results are similar to those found by Reichert et al., (2020), where they found no consistency in learning speed between an initial and reversal discrimination experiment. On the one hand, the lack of consistency is not surprising, as initial and reversal learning may be underpinned by different cognitive processes (Schoenbaum et al., 2002; Dalley et al., 2004), despite the measurement methodology being identical. On the other hand, environmental factors beyond those measured in this experiment may be influencing performance (Reichert et al., 2020), such that there is no rank-order differences across the population. These factors driving changes in motivation and engagement may be guided by weather (Sergio, 2003; Elkins, 2010), what they ate previously (chapter 2), whether they are anxious after a predator attack (chapter 4), what their mate or flock members are doing may influence performance.

Conclusion

Learning performance, as it pertains to foraging, is contextually dependent on distance between foraging patches, as well as individual attributes such as species, sex, and age. The lack of behavioural consistency within the experiments indicates initial and reversal learning is underpinned by separate processes. The specifics of experimental design for cognitive tests in the wild are important, because individuals perform differently even with small differences like an extra two m between devices. Additionally, these design challenges can be leveraged to create experiments examining effects of ecological factors like the spacing of resources on cognitive performance.

Appendix

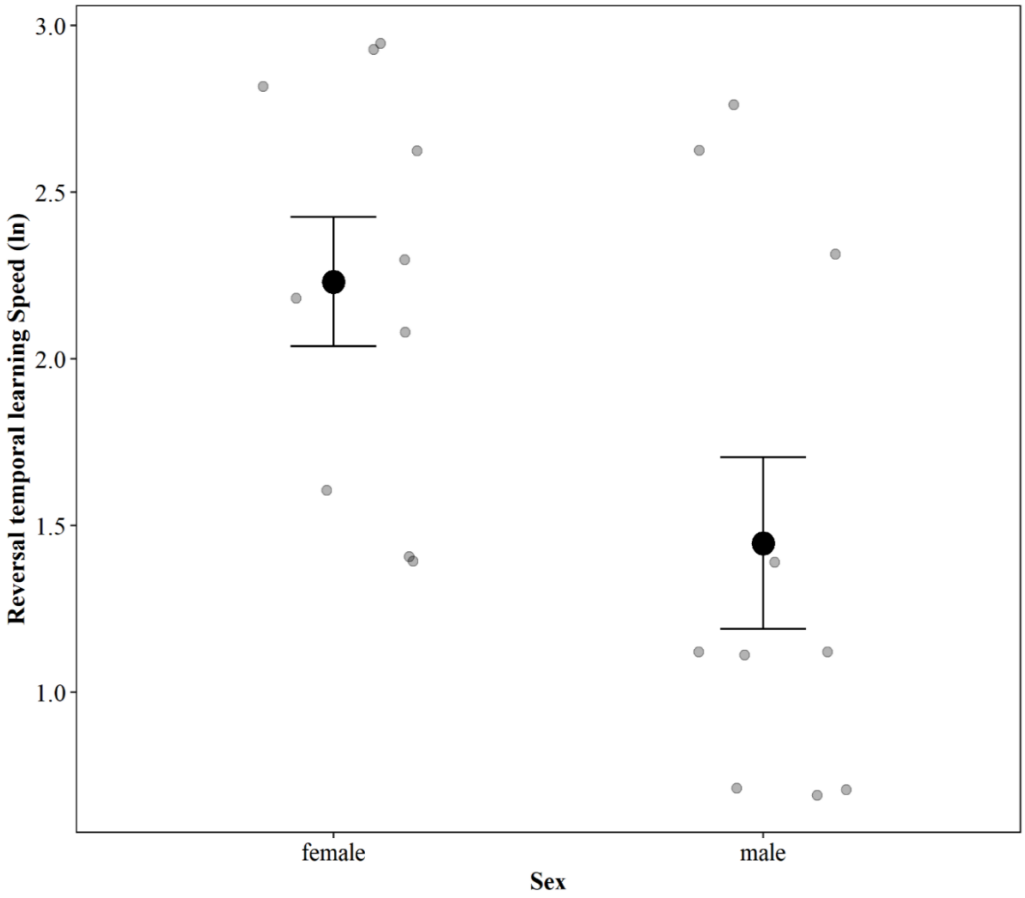

Figure A1 The sex differences in temporal reversal learning speed. Lower values represent faster learning. Points represent individual birds (points have been jittered along the x-axis) and the large point represents the mean and the t-bars represent the standard error from the mean.

Table A1 Model output from the general linear model with factors affecting initial learning speed. Model ran on the subset of birds with known sex (n = 55, d.f. = 49). Terms below the dashed line were not retained in the minimum adequate model.

Term	Coefficient	Standard error	Z	P
Intercept	2.246	0.263	8.545	<0.01
Distance[a]	1.170	0.356	3.288	<0.05

Sex[b]	-0.182	0.359	-0.506	0.615
Age[c]	0.507	0.401	1.264	0.213
Own feeder malfunctioning time (hrs)	0.133	0.084	1.586	0.200
Other feeder malfunctioning time (hrs)	0.104	0.060	1.722	0.092
Feeder position[d]	-0.273	0.361	-0.756	0.454

[a] three metres (reference level one metre), [b] male (reference level is female), [c] adult (reference level is juvenile), [d] edge (reference level is centre)

Table A2 Model output from the general linear model with factors affecting memory. Model ran on the subset of birds with known sex (n = 34, d.f. = 22). Terms below the dashed line were not retained in the minimum adequate model.

Term	Coefficient	Standard error	Z	P
Intercept	0.827	0.241	3.434	0.002
Distance[a]	0.116	0.208	0.555	0.609
Sex[b]	0.242	0.186	1.298	0.208
Age[c]	-0.223	0.214	-1.039	0.310
Initial learning speed	0.000	0.001	0.124	0.902
Feeder position[d]	0.237	0.206	1.150	0.262
Own feeder malfunctioning time (hrs)	-0.008	0.041	-0.185	0.855
Other feeder malfunctioning time (hrs)	0.019	0.048	0.398	0.695

[a] three metres (reference level one metre), [b] male (reference level is female), [c] adult (reference level is juvenile), [d] edge (reference level is centre)

Table A3 Model output from the general linear model with factors affecting reversal learning speed. Model ran on the subset of birds with known sex (n = 33, d.f. = 24). Terms below the dashed line were not retained in the minimum adequate model.

Term	Coefficient	Standard error	Z	P
Intercept	1.603	0.268	5.980	0.000
Distance[a]	0.769	0.339	2.270	0.086
Sex[b]	0.349	0.185	1.880	0.072
Own feeder malfunctioning time (hrs)	0.091	0.045	2.040	0.053
Other feeder malfunctioning time (hrs)	0.112	0.036	3.110	0.005
Age[c]	0.135	0.253	0.534	0.599
Initial learning speed	-0.004	0.025	-0.153	0.880
Memory	-0.022	0.036	-0.602	0.554
Feeder position[d]	-0.106	0.245	-0.433	0.670
Initial learning speed*Distance[a]	0.004	0.025	0.161	0.874

[a] three metres (reference level one metre), [b] male (reference level is female), [c] adult (reference level is juvenile), [d] edge (reference level is centre)

Table A4 Model output from the general linear model with factors affecting temporal learning speed. Model ran on the subset of birds with known sex (n = 24, d.f. = 12). Terms below the dashed line were not retained in the minimum adequate model.

Term	Coefficient	Standard error	Z	P
Intercept	2.720	0.219	12.400	0.000
Distance[a]	-0.722	0.568	-1.272	0.272
Sex[b]	0.446	0.336	1.327	0.209
Age[c]	-0.274	0.376	-0.729	0.480
Feeder position[d] (different)	0.276	0.563	0.490	0.633
Feeder position[d] (edge)	0.357	0.656	0.544	0.597

Own feeder malfunctioning time (hrs)	-0.033	0.063	-0.513	0.617
Other feeder malfunctioning time (hrs)	0.129	0.072	1.783	0.100

[a] three metres (reference level one metre), [b] male (reference level is female), [c] adult (reference level is juvenile), [d] reference level is centre.

Table A5 Model output from the general linear model with factors affecting temporal reversal learning speed. Model ran on the subset of birds with known sex (n = 20, d.f. = 12). Terms below the dashed line were not retained in the minimum adequate model.

Term	Coefficient	Standard error	Z	P
Intercept	2.749	0.163	16.890	0.000
Sex[a]	-0.642	0.204	-3.150	0.008
Own feeder malfunctioning time (hrs)	1.954	0.783	2.500	0.028
Other feeder malfunctioning time (hrs)	0.071	0.013	5.390	0.000
Distance[b]	0.437	0.442	0.989	0.396
Temporal learning speed	0.003	0.023	0.152	0.883
Age[c]	0.121	0.251	0.481	0.643
Feeder position[d] (different)	0.057	0.358	0.158	0.879
Feeder position[d] (edge)	-0.584	0.595	-0.982	0.355

[a] male (reference level is female), [b] three metres (reference level one metre), [c] adult (reference level is juvenile), [d] reference level is centre.

Chapter 6. General Discussion

Cognition is a major driver of animal behaviour, and variation in cognitive performance is likely present in all populations (Rowe and Healy, 2014). Variability between and within individuals, can be a result of cognitive and non-cognitive factors. Recognising and exploring the depth of proximate factors that drive the differences in behaviour is imperative to understanding the adaptive significance and thus evolutionary ecology of cognition. The overarching aim of my thesis was to advance our understanding of the role proximate factors have in shaping cognitive performance and consistency in great tits, by exploring the interplay between physiology, individual characteristics, and environment. Overall I have demonstrated that great tits are sensitive to a range of intrinsic and extrinsic proximate factors, that drive variation in behaviour and cognitive performance in both predictable and unpredictable ways. Below, I will discuss the potential cognitive mechanisms involved in problem-solving performance identified in **Chapter 2**, and how they can be incorporated into our understanding of consistent individual behaviour. With this in mind, I will then discuss the role and consequences of different proximate factors affecting problem-solving and personality examined in **Chapter 2 & 3**. I will then move on to discussing the spatial (**Chapter 4**) and temporal variation (**Chapter 5**) in learning performance, in terms of the effect of naturally occurring, ecologically relevant proximate factors and how new tools can help us collect robust data in greater detail.

Innovative problem-solving

Cognitive mechanisms

Many experimental tasks begin with setting a problem (Kuczaj, 2017), such as an array of filled bird feeders, of which only one is rewarding (Reichert et al., 2020), and measuring how or whether an animal can overcome it (Seed and Mayer, 2017). The aim of these tasks is to tap into a specific cognitive mechanism of the focal individual, such as spatial or discrimination learning. In contrast, problem-solving tasks are increasingly being used to measure innovativeness - behaviours that are entirely novel or expressed in a novel context (Réale et al., 2007) – which is an

important source of phenotypic plasticity and evolutionary change (Griffin et al., 2014). Up until recently, research has predominantly focused on who the innovators are (Morand-Ferron et al., 2011; Thornton and Samson, 2012; Cauchard et al., 2013), rather than how an innovation develops and becomes established as part of an individual's behavioural repertoire. Moreover, there is no consensus as to whether problem-solving involves specific cognitive mechanisms, however this does not preclude cognition from being involved. Results from **Chapter 2** identified the separate measurable behavioural traits that are fundamental to innovation: latency to touch the device, accuracy when interacting with the device, likelihood of solving within a trial, the establishment of that behaviour into the repertoire, and the repetition of the innovative process across different tasks. By breaking down this behaviour into a series of sequential tasks, it allowed me to examine the factors that gave rise to innovation and develop its future use within individuals until it became part of their repertoire. Individual consistency was assessed through repeated presentations and controlled treatments and the results suggest some element of cognitive processing occurring. For example, it was possible to measure accuracy when interacting with the task which has the potential to be a putative cognitive measure, because it may involve trial and error learning through sensory feedback and information processing, where accuracy increases solving, and the positive feedback loop the reinforces this behaviour. Previous studies that have deconstructed problem-solving performance have focused on the behavioural traits hypothesised to help or hinder innovation (Auersperg et al., 2012; Thornton and Samson, 2012; Logan, 2016a; Daniels et al., 2019), but through the research in my thesis I show that by systematically manipulating the information available in problem-solving tasks, it is possible to discover how individuals are processing this information.

Motivation

In **Chapters 2 & 3**, I provide evidence that food-related motivation is instrumental in both problem-solving and exploration behaviour. **Chapter 2** shows robust evidence of multiple positive relationships between food-related motivation and different stages of problem-solving, namely, latency to touch the device, likelihood of solving within a trial and innovativeness. In line with the "necessity drives innovation" hypothesis (Laland and Reader, 1999b), these behaviours were likely

induced by the individuals' energetically challenged state. In comparison, accuracy was the only response variable not influenced by motivation, indicating that at least one aspect of problem-solving is not dependent on any state I measured, and instead probably involves some cognitive capacity (Bókony et al., 2014). The variability in driving forces across the different problem-solving measures suggests that innovative problem-solving is a composite behaviour, which is influenced by at least one state-dependent variable, as well as individual temperament differences. This study revealed important predictors of performance and variability in the forces driving separate measures problem-solving performance, which suggests that innovative problem-solving is a composite behaviour.

The results from **Chapter 2** have implications for how to interpret the results in **Chapter 3**, whereby birds who received the insect diet were less likely to solve the insect-rewarded problem-solving task. Although myself and colleagues have reported that problem solving in birds on the insect diet was associated with microbiome profiles (Davidson et al., 2020), I cannot rule out the possibility that those birds that did not solve were less motivated to do so because of their access to mealworms throughout the experiment. To control for such an explanation, I provided birds a freely available waxworm, and found that those who consumed it were no more likely to solve than those that did not. In some studies (including **Chapter 2**), consuming a freely-available worm is interpreted as an individual being motivated to participate in the task (van Horik and Madden, 2016; Davidson et al., 2020). While it is important to distinguish between individuals who failed at a task, versus those who did not participate, it remains possible that I am misinterpreting being motivated to participate, and cognitively and behaviourally engaging with the task. Consuming a food item near or on a task gives us no observable indication as to whether that individual was equally motivated to engage in the mental processes of that task itself. If the task was recorded on video, I may have a better indication of their engagement in the task, but logistically it was not possible to record their behaviour at the devices. I recommend that future studies attempting to quantifying problem-solving behaviour should use the same methodology as **Chapter 2**.

Controlling for food-related motivational effects generally is unlikely to be straightforward. When food depriving animals, we assume when we are controlling

for motivation, that all individuals are converging to the same level of motivation. But just as we find individual variation in behavioural traits (Dingemanse et al., 2002; Sih et al., 2004), motivation may also vary between individuals. For example, rank order differences may be present, so despite individuals being motivated to the same extent (i.e. the treatment was equal), individual variation may remain, because each individual's initial motivational level (or starting point) was different. Similarly, they may have different thresholds and so motivation has increased, but the individual differences remains the same. This presents a unique challenge for studies involving innovation, since if successful, an animal would need to be presented with a different task for their second treatment. Given the extent that motivation affects behaviour, future work to account for rank order differences on motivation, could compare the behaviour of the same individual using repeatability analysis, across different treatments.

Personality

Innovative behaviour can be mediated by personality, which constrains how an animal behaves and reacts throughout time and space (Réale et al., 2007). However the results of different studies testing the relationship between personality and problem-solving performance are often in conflict (Cole et al., 2011; Guillette et al., 2011; Amy et al., 2012; Zandberg et al., 2017). Thus, the absence of a relationship between personality and problem-solving performance in this thesis is not unusual. In **Chapter 2**, personality was selected across multi-generations for three measures of boldness - two novel object tests (latency to touch the novel object) and exploration of a novel environment - but it had no effect on the latency to touch the multi-access problem-solving device. A recent meta-analysis investing the link between cognition and a range of personality traits including exploration behaviour, boldness, activity, aggression and sociability, found a significant but small relationship between personality and cognition, the direction of which varied depending on the study (Dougherty and Guillette, 2018). Moreover, this same study found that the link may be dependent on the type of personality and cognitive measure. This would suggest that despite the robustness of the selected personality measures, it does not translate into an effect on problem-solving performance, but why this is the case remains unknown.

Fatty acid profiles

In **Chapter 3**, I provide evidence that individual behavioural variation in captive-held wild great tits was influenced by diet and fatty acid profiles. Above I discussed how birds on the insect diet were less likely to solve after consuming only insects for two weeks. In this same study there was a negative correlation between arachidonic acid (AA) and personality, where more exploratory individuals had a lower proportion of AA in their red blood cells. Much of what is known regarding the role and function of AA in cognition and behaviour is from studies in biomedical research (Wainwright, 2002; Rapoport, 2008; Bazinet and Layé, 2014), with a focus on human participants (Fontes et al., 2015). For example, AA and docosahexaenoic acid (DHA) account for 20% of the fatty acids found in the mammalian brain (Contreras et al., 2000) and are necessary for normal brain development and function (Spector, 2001). In adult humans high rates of AA in the brain phospholipid membrane are associated with bipolar disorder (Rapoport, 2008). While in hyperactive human children, the proportion of AA and of DHA was significantly lower than their non-hyperactive counterparts (Mitchell et al., 1987). In comparison to the breadth of research in humans, the ecological relevance of fatty acids in wild animals is relatively understudied. For this reason the implications of the findings from **Chapter 3** are particularly interesting because it provides an opportunity for the study of physiological drivers of animal personality and cognition. For example, the principal personality measure taken in this research group is exploration behaviour in a novel environment, which is consistent across time and contexts (Réale et al., 2007) and has been shown to be genetically heritable (Dingemanse et al., 2002). As of yet, there is no identifiable physical mechanism or pathway to explain differences in exploration behaviour and so these differences are often classified as inherent (Cole and Quinn, 2012; Carter et al., 2013a). However I found that regardless of their diet, fast explorers had a lower proportion of AA in their red blood cells. One possible cause for this, is that fast explorers were selectively mobilising this fatty acid from adipose tissue (Raclot, 2003; Price et al., 2008, 2013), which may result in higher activity levels and a higher rate of AA breakdown. Regardless of the exact processes, this association between exploration behaviour and proportion of arachidonic acid is worthy of further investigation, in particular the direction of this causal relationship. In terms of the lack of evidence

that changes to the fatty acid profile of birds are linked to problem-solving performance, there remains a range of unexplored nutritional aspects not measured from fatty acids, such as calorific content and oxidative stress that could influence performance.

Hunger levels and food consumption naturally fluctuate throughout the day and lifecycle of animals. Despite this variability, work from this thesis demonstrates that food-related motivation is a major driver of repeatable consistent individual differences in problem-solving. However, the longevity of the effects of food and motivation on individuals remains unknown, and should be considered as the next logical step in future research. Can naturally cycling proximate factors cause prolonged or permanent differences between individuals? Are there within and between individual differences in response to chanages in hunger levels? It is under this framework, that we can further our understanding the psychological processes, behavioural traits and proximate factors that underpin innovation.

Sex and age

Ecological and sexual selection pressures may be driving differences in cognitive performance and behaviour (Dougherty and Guillette, 2018; Wallace et al., 2020). For example, in winter, great tits must compete for access to clumped and limited food resources, and as a result suffer substantial mortality from starvation, and is particularly evident among subordinate individuals (Gosler, 1996), such as females and juveniles (Gosler, 1993). The necessity drives innovation hypothesis, states that individuals who are less competitive are more likely to innovate, as they need to find novel methods of accessing a resource they would otherwise be excluded from (Laland and Reader, 1999a). Previous studies have shown a negative correlation between competitive ability and problem-solving success (Cole and Quinn, 2012), as well as a positive correlation between female problem-solving success and reproduction (Cole et al., 2012); however across **Chapters 2 & 3**, there was no conclusive evidence of sex or age differences in innovative problem-solving performance. This lack of sex or age differences has occurred in previous research in great tits (Serrano-Davies et al., 2017; Zandberg et al., 2017) and in other bird and mammal species (Bouchard et al., 2007; Benson-Amram and Holekamp, 2012; Dougherty and Guillette, 2018), which suggests that necessity via competition is

not solely responsible for innovativeness. Instead, lack of sex and age differences may be due to a species level trait, since instances of innovative behaviour are more common in generalist species (Bonier et al., 2007; Wong and Candolin, 2015), as they seek out novel habitats and resources.

Spatio-temporal cognitive performance and memory

The final two data chapters in this thesis focused on established cognitive mechanisms, namely learning and memory, in a spatial, discrimination and temporal paradigm, because approaching learning and memory from different starting points may provide a more comprehensive understanding of individual variation and the proximate factors affecting learning (Healy and Braithwaite, 2000).

Perceived predation risk and cognitive performance

Variation in intensity of predation pressure is known to have substantial impact on the evolutionary ecology of different species (Brown and Braithwaite, 2005), and despite the ubiquity of this proximate factor in the animal kingdom, the effect that predation risk may have on individual cognitive performance has been very much understudied. Context plays a dynamic role in the trade-off between vigilance and foraging efficiency; for example, increased hunger levels correlate with a reduction in predator vigilance (Bachman, 1993), hunger levels increases, but intrusion rate decreases seasonal territorial vigilance (Ydenberg and Krebs, 1987), while the "many eyes" hypothesis suggests that gregarious living evolved as a result of collective vigilance (Olson et al., 2015). The results from **Chapter 4** highlight the subtle effect that predation risk has on cognitive performance while foraging, in that variation in the level of predation risk did not cause differences in learning or reversal learning speed, however birds subject to the highest risk of predation performed better in their reverse learning task than initial learning task, and had relatively poor memory. Together these results suggest that context may influence cognitive performance, and specifically the extreme situation of being exposed to an actual predator that may induce changes in cognitive performance, as well as type of cognition used. For example, during a foraging bout, investing time and energy into learning and memory may increase exposure to predation threat, as animals follow the same route or consistently attend the same location (Krebs and

Davies, 1987; Davies et al., 2012), but behaving flexibly while predation risk is high allows animals to continue foraging and mitigate some of the predation risk.

Trade-offs in cognitive performance across different mechanisms may only be expressed under certain environmental stimuli, such as harsh climate (Croston et al., 2016) and in my case predation risk, where the intensity of proximate factors may induce a trade-off between different cognitive mechanisms (Chittka et al., 2009; Ducatez et al., 2015a). Here I present two examples of when this could be occurring in the high predation risk group, but not in the low or medium risk groups. First, the negative correlation between reversal learning and memory may occur because memory capacity is limited, where old memory prevent or interfere with the acquisition of new memories (Anderson and Neely, 1996; Jacoby et al., 2001; Wixted, 2004). Why this correlation is only present in the high-risk group is not clear. However research by Dalesman et al., (2015) showing foraging-related memory is negatively correlated with predation risk memory in multiple populations of pond snails (*Lymnaea stagnalis*) suggests selection may be acting on plasticity in foraging cognition and antipredator behaviour. The second piece of evidence for a trade-off is the negative correlation between initial and reversal learning in the high-risk predation treatment, which suggests that behavioural flexibility allows prey to manage under high predation risk. Under naturally high occurring predation risk, this trade-off could offset negative population-level effects (Toscano, 2017). Evidence of these two correlations between reversal learning and memory, and initial and reversal learning suggest predation threat level may be driving two trade-offs between vigilance and foraging related cognitive performance. In contrast, in **Chapter 5**, where it was not possible to measure predation risk and so it was not controlled for, there was no evidence of a correlation between behavioural flexibility (reversal learning) and memory, and initial and reversal learning, which may mean that they are only evident when under harsh or stressful conditions.

The lack of variation in learning performance between the predation risk treatment groups in **Chapter 4** contrasted with previous work conducted on fish (Brown and Braithwaite, 2005; Brydges et al., 2008; Burns and Rodd, 2008). For example, Brown and Braithwaite (2005) found that fish in low predation environments had better learning performance across a number of different spatial learning measures.

This difference in cognitive performance in response to predation risk between birds and fish may be a result of adaptive specialisation (Magphail and Bolhuis, 2001), where the cognitive abilities of a species evolved to meet their way of life, and as a result the signal for low predation pressure is perceived and affects birds and fish in different ways. It is worth noting that there was a tendency for an effect of predation treatment on learning speed, but the low sample size in this experiment reduced the power to examine this variability. Therefore, I think this experiment could be repeated with an increased sample size across all three treatment groups, perhaps increasing the strength of the perceived predation risk. It would be interesting to investigate whether the results between the two iterations of the experiment are repeatable, in particular whether predation risk level has no effect on learning performance or whether the effect wasn't detectable because of the sample size. Nevertheless, this work highlights how the same proximate factor may differently influence cognitive performance between individuals.

Proximate factors influencing where and when learning

The previous chapters allowed for controlled manipulations in a captive environment; however the way in which animals learn and remember may be dependent on whether they are free-living or in captivity (Benson-Amram et al., 2013; Cauchoix et al., 2017; Vardi et al., 2020), and may also be subject to evolutionary processes that affect natural variation in behaviour (Morand-Ferron et al., 2016). Therefore in my final chapter, I took the spatial feeder array to the field, to explore proximate factors that may affect cognitive mechanisms underlying foraging behaviour, namely discrimination learning, temporal learning, reversal learning and memory. This field study allowed me to consider species differences and interactions between blue tits (*Cyanistes caeruleus*) and great tits, as from an ecological perspective, it's an important aspect to consider as during the winter they naturally form mixed species flocks (Gosler, 1993).

The first novel aspect of this study was the distance treatment (1 m or 3 m feeding array). Contrary to my expectation that a greater feeder distance would encourage birds to invest in learning their rewarded feeder given the potential cost of making errors when feeders were further apart, I found that birds performed significantly better when the feeders were 1 metre apart. This was the case for initial and reversal

discrimination learning, but not initial and reversal temporal learning. One potential interpretation that arose due to this unexpected result was that perhaps birds were relying on retinal snapshots to learn their rewarding feeder (Collett et al., 1986), which is a mechanism for how individual perception influences cognitive performance. An animal can use the difference between a stored retinal image and their current retinal image to guide their behaviour. Bees and rodents rely on retinal snapshots when navigating spatial arenas association with food locations (Cartwright and Collett, 1983; Lee and Spelke, 2010). Although tits have yet to be tested on whether they use retinal snapshots, the fact that they performed better when feeders were spaced closer together could be explained by such a navigational mechanism. Furthermore, this interpretation highlights how cognitive mechanisms may be working in tandem, for example discrimination learning (a mechanism in itself), might be influenced by the mechanism used for perception. The second interpretation I provide for the effect of distance in learning performance, refers to a trade-off between flock density and vigilance, where closer feeders result in higher density flocks, providing better vigilance and allowsing for individuals to focus on learning. A future direction for this line of research involves examining the social dynamics that may occur at the feeder, in order to investigate whether group size influences learning, producer-scrounger effects, species affect others from learning (e.g. learn better in a single species group vs mixed species group).

Great tits have the capacity for behavioural traits identified in specialist species, and my temporal findings provide further evidence of this, as I show for the first time, that two generalist passerine species are capable of temporal learning. With the results from **Chapters 4 & 5**, it can now be said that great tits are capable of demonstrating the three components of episodic-like memory in isolation (Clayton and Dickinson, 1998), namely what (discrimination learning), where (spatial learning) and when (temporal learning). Episodic-like memory requires that animals flexibly and repeatedly update what-where-when recollection into distinct new memories/episodes. I show that they remember where food is and whether it's available in the afternoon or morning, and they can switch this information in the context of which feeder. In the context of the evolution of cognition, this is an important finding, since evidence of episodic-like memory in birds has previously only been demonstrated in specialist species, where episodic-like memory is a

requisite of survival, such as scrub jays (*Aphelocoma coerulescens*) (Clayton and Dickinson, 1998), chickadees (*Poecile atricapillus*) (Feeney et al., 2009) and rufous hummingbirds (*Selasphorus rufus*) (Marshall et al., 2013). However, in my study I did not separate the *what* component from the *where* component, which could be achieved by using different food items. Future work research could combine these tasks to investigate whether great tits are capable of episodic-like memory.

Sex and age

In contrast to innovative problem-solving performance, males outperformed females across two measures of reversal learning performance, spatial (**Chapter 4**) and temporal (**Chapter 5**). This asymmetry in performance between the sexes may reflect differences in reproductive investment: while females during the breeding season focus primarily on parental care, males have a more diverse role to play and this may necessitate a greater need for behavioural flexibility to move efficiently and flexibly throughout their territory than females (Jacobs et al., 1990). Further research is necessary to confirm whether sex differences in reversal learning are influenced by seasonality.

Unlike sex, age differences in learning performance were more variable. Adults are equally capable of initial and temporal discrimination learning, whereas juveniles are significantly worse at discrimination learning compared to their temporal learning performance, and to adult discrimination performance. In black-capped chickadees (*Poecile atricapillus*) learning performance in the first year of life predicts survival to the following year (Sonnenberg et al., 2019), and this suggests that a greater degree of flexibility in juveniles may be necessary in order to survive (Laland and Reader, 1999a). In contrast, age-related effects were absent from all measures of the spatial learning experiment (**Chapter 4**). Whether the disparity in results across the two chapters was due to the social difference of individual testing, such as social learning (Ashton et al., 2019), displacement (Aplin and Morand-Ferron, 2017) and group vigilance (Cresswell et al., 2003), or the difference in cognitive test paradigm, or indeed the fact that stress levels generally may have been different, remains unknown. Future work could reverse the contexts of these two experiments, where the discrimination task is conducted individually in temporary captivity, while the spatial task is run in the wild.

Conclusions

In this thesis, I provide new insight into a variety of underexplored proximate factors that explain individual variation in cognitive performance and its associated behaviour. When assessing individual variation in problem-solving performance, it is vital to break this composite behaviour down into separate measurable parts. The discovery of positive feedback loops, repeatability and pseudo-repeatability illustrates the importance of this methodology. Furthermore, this research demonstrates that food-related motivation can influence performance during an experiment and it in fact explains much of the between individual variation, which to my knowledge has never been shown previously. While this methodology is labour intensive, I advocate for its future use in order to generate more informed measures of individual problem-solving performance and to fully understand the proximate forces driving variation in this behaviour. By understanding the effect that food has on the individual after it is consumed, we can better understand variation in behaviour. I have presented evidence of the influence that proximate factors have on problem-solving performance and personality, by investigating how diet and fatty acid composition may be linked to behaviour. In particular, I have identified arachidonic acid as a potential driver of personality, and future work should involve targeted manipulations of fatty acids shown to correlate with variation in behaviour, in order to understand the causality of this relationship. Variation in proximate factors may have subtle individual effects on cognition performance. I show that only high predator threat level influences cognitive performance in a spatial foraging task. This work highlights the importance of varying intensity in external proximate factors, and how this may influence behaviour. Furthermore, there was a trade-off between behavioural flexibility and memory. Future work could focus on disentangling whether reduced memory retention in individuals under high pressure arises from causation or correlation. Finally, I examined the learning capabilities of great tits and blue tits in the wild. This research shows for the first time, that both species are capable of temporal learning. The final two data chapters revealed how different external proximate factors influence a diverse range of learning measures and illustrate how device design features can be leveraged to create experiments examining effects of ecological factors like the spacing of resources and temporal variability on

cognitive performance. Overall, my thesis demonstrates how cognitive performance is dependent on complex sources of variation underlying single traits, and predicting the selective consequences of this variation challenging, especially in the wild. Disentangling the interplay between these two aspects will further develop our knowledge of the evolution of behaviour and cognitive performance.

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